

PREDICTING POTASSIUM UPTAKE FOR PINUS ELLIOTTII ENGLEMAN.  
VAR. ELLIOTTII USING DIFFUSION/MASS-FLOW  
NUTRIENT-SUPPLY THEORY

BY

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"Blessed is the man who trusts in the Lord and whose trust is the Lord. For he will be like a tree planted by the water, that extends its roots by a stream and will not fear when the heat comes; but its leaves will be green, and it will not be anxious in a year of drought nor cease to yield fruit."

Jeremiah 17:7-8

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Major Department: Soil Science Department

The application of diffusion/mass-flow theory to potassium (K) uptake by slash pine (Pinus elliotii Engelm. var. elliotii) seedlings from soil of low K-supplying potential is presented. Simulations for K uptake were evaluated by both the Barber-Cushman model (BCM) and the Baldwin-Nye-Tinker model (BNTM) under both greenhouse and field conditions. Potassium uptake was overpredicted by 31 to 50% in greenhouse studies; overestimates, however, can be attributed to non-uniform distribution of roots along pot walls. Simulations underpredicted uptake by 17 to 52% for seedlings grown in the field. Although external fungal hyphae were abundant in the field, their contribution to K uptake was not incorporated, suggesting the potential importance of such hyphae in uptake processes. Predictions of K uptake by seedlings grown at a tree nursery were excellent when

fertilizer amendments were included. The BNTM, based on simplifying assumptions and the BCM, predicted similar K uptake values.

As compared with entire root systems, woody roots of slash pine were an effective surface for water, K and rubidium (Rb) absorption in solution cultures. Determining separate parameters for woody and white roots did not improve K uptake predictions over those for entire root systems.

Slash pine seed sources affected root uptake parameters as well as the root's ability to selectively absorb K and Rb.

Incorrect definitions of soil buffer power can lead to erroneous estimates of solute diffusion coefficients and nutrient replenishment in soil solutions: factors important for determining rates of nutrient supply in uptake models.

Sensitivity analysis showed that root growth and initial K concentration in soil solution were the two most important factors affecting K uptake by slash pine. Soil processes, however, appeared to limit K uptake for these soils. Monte Carlo procedures applied to two harvests in the field indicated that simulated estimates of uptake had CV's ranging from 34 to 64%.

The successful validation of K uptake under these conditions suggests that future applications of this approach may contribute to understanding the nutrition of rotation-aged trees. Reliable estimates of rooting densities must be included, however, together with information on multiple soil horizons.

## CHAPTER 1 GENERAL INTRODUCTION

Evaluating the nutritional importance of the complete soil profile for slash pine (Pinus elliotii Engelm. var elliottii) growth requires an understanding of the factors affecting nutrient uptake. An initial factor is the vertical extent and density of the root system. For slash pine trees growing on poorly-drained Spodosols, vertical root distributions ranged from  $0.22 \text{ cm cm}^{-3}$  in the surface to  $0.01 \text{ cm cm}^{-3}$  at a 2.4 m depth (Van Rees and Comerford, 1986). Fine roots (i.e.,  $< 2 \text{ mm}$  dia.) on these sites were found to proliferate in the argillic horizon (1 m depth), suggesting that this subsoil horizon may be significant for tree nutrition. The testing of this hypothesis, that subsoils are important to tree nutrition, has resulted in a variety of studies (Comerford et al., 1984).

For slash pine on a flatwoods site, uptake of strontium (Sr) was used as a measure of "root activity" in different soil horizons (Van Rees and Comerford, 1986). During the summer months, roots in the argillic horizon were shown to absorb more Sr than roots in the A horizon, as reflected by Sr levels in the foliage (Van Rees and Comerford, 1986). This technique, however, remains at best only a qualitative estimate of the root's potential to acquire nutrients. A more

quantitative approach, that would include rooting densities and the ability of soil horizons to supply water and nutrients, is desired.

Integration of such factors in efforts to quantify nutrient uptake has been accomplished through use of mathematical models. Simulations were based on the theoretical considerations of the diffusion/mass-flow processes for ion transport to, and uptake by, a single root growing in soil (Bouldin, 1961; Passioura, 1963; Nye and Spiers, 1964; Nye, 1966a; Nye and Marriott, 1969). Since then, root growth has been incorporated into nutrient uptake models (Baldwin et al., 1973; Brewster et al., 1976; Claassen and Barber, 1976). Such models have been validated only for potassium (K), phosphorus, magnesium, cadmium and zinc uptake for agronomic crops grown on fertilized soils (Schenk and Barber, 1980; Silberbush and Barber, 1983, 1984; Mullins et al., 1986; Rengel, 1988).

Parameters estimated from plant species and conditions for which models have previously been validated, however, may not necessarily represent the parameters used for slash pine trees growing on poor nutrient-supplying soils of the southeastern coastal plain. One of the important differences is the morphology of the root systems. Slash pine root systems include unuberized root tips to large woody roots with secondary growth; consequently, differences in root morphology could influence nutrient and water uptake to varying extents. Little information is available, however,

on the absorption of water or nutrients by woody and white root systems.

Although the general hypothesis is that subsoils are important to tree nutrition, a first step in testing this hypothesis is to determine if the theoretical approach for nutrient uptake, based on diffusion/mass-flow processes (via the Barber-Cushman and Baldwin-Nye-Tinker models) can be applied to K uptake by slash pine seedlings grown in surface horizons of a flatwoods Spodosol.

Therefore, the following research addresses the application of the two mechanistic models to K uptake.

Each of the following four chapters is an independent manuscript, intended for journal publication, relating separate aspects of parameter estimation and validation of the diffusion/mass-flow theory for K uptake by slash pine seedlings.

Chapter 2 is a study of the absorption of potassium by root surfaces of slash pine grown in solution cultures, described in terms of Michaelis-Menten kinetic parameters.

Chapter 3 addresses the effect of differing root morphology on uptake; and tests specifically the hypothesis that woody (suberized) roots of slash pine offer an effective surface for water and K absorption and, therefore, should be considered in nutrient uptake models.

Chapter 4 clarifies the use of soil buffer power, a soil parameter used to index the soil's ability to replenish ions to the soil solution. Several definitions exist and incorrect

applications could result in erroneous estimations of ion diffusion and nutrient uptake.

Chapter 5 incorporates the results of the previous three chapters in an attempt to validate K uptake through existing theories of nutrient uptake for slash pine seedlings grown in soils of low K-supplying potential under greenhouse and field conditions.

CHAPTER 2  
UPTAKE KINETICS AND SELECTIVITY FOR POTASSIUM AND  
RUBIDIUM BY SLASH PINE ROOTS

Introduction

The mobility of nutrients in soils and their subsequent absorption by root surfaces reflect dynamic and complex processes. These processes have been linked together by relating the rate of ion uptake by the root to the ion concentration external to that root. This relationship, however, has been difficult to measure in soil; therefore, most ion uptake studies have been undertaken in solution cultures.

Epstein and Hagan (1952) hypothesized that ion influx, particularly at low solution concentrations ( $<1$  mM), could be empirically described by Michaelis-Menten kinetics:

$$I_n = I_{\max} C_L / (K_m + C_L) \quad [1]$$

where  $I_n$  is the ion influx rate,  $I_{\max}$  is the maximum ion influx rate,  $C_L$  is the concentration of the ion in solution and  $K_m$  (the Michaelis constant) is the ion concentration at which  $I_n$  is one-half  $I_{\max}$ . Michaelis-Menten kinetics were generally determined either by short-term absorption studies using excised roots and isotopically labelled ions, or by long-term studies using intact plants and a graded series of nutrient solutions maintained at constant concentrations (Epstein,

1972; Nye and Tinker, 1977). Claassen and Barber (1974) simplified the procedure by measuring the rate of nutrient depletion from a solution. Different procedures for analyzing the depletion curves with respect to uptake parameters have also been presented by Wild et al. (1979), Bhat (1981) and Mullins and Sommers (1986). Nutrient uptake investigations utilizing this procedure, however, have largely been restricted to annual plants or herbaceous perennials (Epstein, 1972; Nye and Tinker, 1977), and some deciduous fruit crops (Bhat, 1981; Rosen and Carlson, 1984), with relatively little work on forest tree species.

Nutrient absorption by plant roots has also been shown to be negatively correlated to the internal concentration of the ion in the root tissue. This internal regulating process, or negative feedback mechanism, suggests that roots are capable of acclimating to the level of nutrient supply over a wide range of external ion concentrations (Jensen and Pettersson, 1978). Such a mechanism has been demonstrated primarily with annual plants, notably for barley roots with potassium (K) (Glass, 1975; 1977), phosphorus (P) (Drew et al., 1984), and chlorine (Cl) (Lee, 1982); for soybean roots with P (Borkert and Barber, 1983); and for corn roots with K (Claassen and Barber, 1977). Jensen and Pettersson (1978) likewise found that K influx decreased with increasing K concentrations for roots of Pinus silvestris, Betula verrucosa and Picea abies. Due to the effect of tissue concentration

on nutrient influx, Siddiqi and Glass (1982) proposed a modification of the Michaelis-Menten equation which incorporated both the external and internal ion concentrations to calculate ion influx.

Rubidium (Rb), a cation similar to K in valence, ionic radius and molecular diffusion coefficient (liquid), has often been substituted for K in order to make inferences about K absorption, transport and accumulation in plant tissues (Lauchli and Epstein, 1970). Evans and Sorger (1966) presented evidence that Rb could replace K in many biological processes. The substitution of Rb as a tracer for K, however, implies that plant roots absorb and transport these two ions indiscriminantly. A majority of the literature demonstrates that K and Rb are selectively absorbed and transported, in studies ranging from marine algae to excised and intact root systems of various annual plants (Menzel and Heald, 1955; West and Pitman, 1967). Correction factors, therefore, would be necessary if Rb tracer studies were to be used to accurately predict K absorption by or transport in plants. Despite the evidence for annual plant species, discrimination between K and Rb has not been investigated for woody perennial plants.

The purpose, therefore, of this study was to (i) determine the influx of K and Rb into intact roots of slash pine (*Pinus elliottii* Engelm. var. *elliottii*) seedlings from solution cultures, using Michaelis-Menten kinetics; (ii) determine the effect of internal root K concentrations on K

influx; and (iii) determine whether or not K and Rb are selectively absorbed by roots of slash pine.

### Materials and Methods

#### Seedling Collection and Conditioning Prior to Solution Culture Experiments

Experiments were conducted over a 3-year period and the seedlings collected each year were obtained from different seed sources (Table 2-1). For each experiment, fifty 1-year old slash pine seedlings were harvested from a commercial tree nursery in Archer, FL, root-pruned and transferred to a 35 L tank containing an aerated, dilute, nutrient solution of pH 4.5 (Table 2-2). Seedlings harvested for the June experiment were cold-stored for 1 month prior to transferring to nutrient solution. Captan was mixed in the nutrient solution on the first day and seedlings were removed the next day, rinsed, and transferred to a new nutrient solution. The nutrient solution was replenished every four days during the following 6-week period. Root initiation began sometime after the first week in solution.

The morphology (adhering to the terminology of Sutton and Tinus, 1983) of the newly-grown (non-woody) roots consisted of two forms: white roots that were assumed to be unsuberized, located towards the root tip, and brown-colored roots located behind the white root zones. Whether the roots were brown as a result of suberin deposition or of degeneration of the epidermis and cortex tissues was not

Table 2-1. Description of the seed sources used in the experiments.

Year of Experiment	Seed Source	Description
1985	1	Seed collected during 1983 in Florida; high-growth clones
1985, 1986	2	Seed collected during 1984 in Florida; general collection
1987	3	Seed collected during 1984 in Alabama; high-growth and high-rust resistant clones

Table 2-2. Concentrations of ions in the pH 4.5 nutrient solution.

Element	Concentration	Element	Concentration
	----- $\mu$ M -----		----- $\mu$ M -----
Nitrate-N	90	Borate-B	0.24
Potassium <sup>a</sup>	77	Iron	0.20
Calcium	75	Manganese	0.02
Ammonium-N	20	Zinc	0.02
Phosphate-P	20	Molybdate-Mo	0.005
Rubidium <sup>a</sup>	12	Copper	0.005
Magnesium	10		
Sulphate-S	10		

a Supplied as chlorides.

determined. Roots of seedlings obtained from the nursery were classified as woody.

Forty-eight hours prior to each depletion experiment, all seedlings were transferred to a nutrient solution lacking K and Rb.

#### Depletion Experiments

Six depletion experiments were conducted using different initial concentrations of K and Rb (Table 2-3). Experiments 3, 4 and 5 were repeated using the same seedlings. Each treatment consisted of five seedlings (with intact root systems) in a 2 L plexiglass pot containing 1 to 1.4 L of aerated nutrient solution. The tops and sides of each pot were covered to reduce evaporation and to shield the roots from light. Marriotte flasks, filled with distilled water, were connected to each pot in order to maintain a constant solution volume. The seed source, root lengths, seedling weights and greenhouse environmental conditions for each experiment are presented in Table 2-3.

Potassium and Rb concentrations in solution were measured hourly to determine their rates of depletion from solution (Claassen and Barber, 1974). Experiments 1 and 2 were 10 hours in duration, while experiments 3, 4, and 5 were 2 to 3 days in length. An example of a depletion curve is presented in Fig. 2-1. Solution samples were refrigerated until time of analysis. Potassium and Rb were analyzed by atomic absorption spectroscopy with 2% cesium to suppress ionization.

Table 2-3. Experimental setup and greenhouse environmental conditions for each depletion experiment.

Experiment and Date	Initial Concentration K	Rb	Number Reps	Shoot Dry Weight <sup>a</sup>	Root Length <sup>a</sup>	Temperature			
						Soln		Air	
						Min	Max	Min	Max
	-- μM --			---- g ----		-- cm --		----- °C -----	
	----- Seed Source 1 -----								
1. 30 July 1985	70	4	3	10.81±0.54	1440±246				
	70	7	3	11.25±0.21	1239± 88	28	29	26	37
	70	11	3	12.35±0.64	1297± 62				
	----- Seed Source 2 -----								
2. 25 Sept. 1985	75	0.2	3	7.65±0.36	2460± 76				
	70	0.4	3	8.11±0.35	2548±201	25	29	28	38
	70	1.0	3	6.11±0.48	2608±187				
3a. 20-21 June 1986	42	42	2			22	29	25	32
3b. 25-26 June 1986	42	42	2			26	31	31	35
3c. 28-29 June 1986	42	42	2	23.21±3.95	3867±145	24	29	26	36

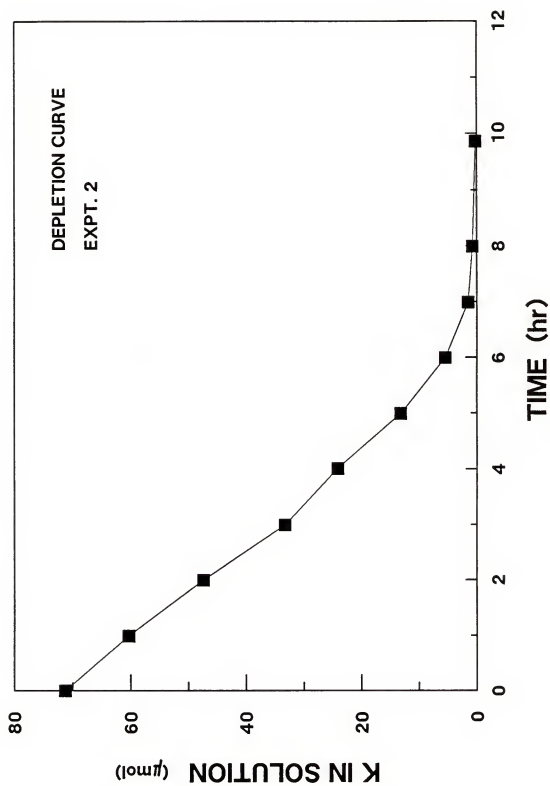
Table 2-3. Continued.

Experiment	Initial Concentration K Rb	Number Reps	Shoot Dry Weight	Root Length	Temperature			
					Soln		Air	
					Min	Max	Min	Max
	-- $\mu$ M --		----- g -----	-- cm --	----- °C -----			
			----- Seed Source 3 -----					
4a. 6-7 April 1987	70 6 70 10 70 70	3 3 3			25	29	25	26
4b. 7-8 April 1987	70 6 70 10 70 70	3 3 3			21	30	25	28
4c. 10-12 April 1987	50 5 48 8 30 27	3 3 3	9.39 $\pm$ 0.96 9.80 $\pm$ 0.44 9.17 $\pm$ 0.35	1929 $\pm$ 302 2022 $\pm$ 318 1887 $\pm$ 313	21	30	25	28
5a. 2-3 May 1987	35 0 70 0 140 0	2 3 2			24	31	27	31
5b. 4-5 May 1987	35 0 70 0 140 0	2 3 2	15.55 $\pm$ 0.84 12.65 $\pm$ 0.29 12.29 $\pm$ 1.57	4689 $\pm$ 196 4453 $\pm$ 429 4889 $\pm$ 557	23	31	25	31

a/ Measurements taken at the end of the experiment; means and SE.

a/ Measurements taken at the end of the experiment; means and SE.

Figure 2-1. A depletion curve for potassium used for determining  $I_{\max}$  and  $K_m$  values.



These depletion experiments were then used for the following analyses:

Calculation of Michaelis-Menten parameters

Ion influx ( $I_n$ ) was assumed to follow Michaelis-Menten kinetics in order to determine the parameters  $I_{\max}$  (the maximum influx) and  $K_m$  (the Michaelis constant) from Experiments 1, 2, 3, 4b,c and 5a,b. Depletion curves were corrected for the amount of K and of Rb removed during sampling. Values of  $I_{\max}$  and  $K_m$  were determined for K and Rb by fitting the depletion curves (concentration vs time) using a least squares procedure (Nielsen and Barber, 1978):

$$t = a - v(C - C_{\min}) / I_{\max} - v K_m (C - C_{\min}) / I_{\max} \quad [2]$$

where  $t$  is the time interval between samples,  $a$  is an integration constant,  $v$  is the solution volume and  $C_{\min}$  is the concentration of the ion when influx is zero.  $C - C_{\min}$  accounts for any ion efflux during the experiment.  $C_{\min}$  was assumed to be  $1 \mu\text{M}$ , based on prior depletion work for slash pine (Beck, 1979).

Values of  $I_{\max}$  were expressed per unit root length, root surface area, root volume, root dry weight and root fresh weight basis. Root lengths were measured by the line-intercept method (Newman, 1966) and an average weighted root radius. Root radii ( $r_o$ ) were calculated for taproots, woody and newly-grown roots by:

$$r_o = [F_{wr} / \pi L]^{\frac{1}{2}} \quad [3]$$

where  $F_{wr}$  is the fresh root weight and  $L$  is the total root

length at the end of the experiment. Equation [3] assumes a root density of  $1 \text{ Mg m}^{-3}$ . Since fresh weights were not determined for experiments 4 and 5, an average root radius was estimated based on values from the other experiments.

#### Relationship between root tissue concentration and influx

The depletion experiments (Expts. 1, 2, 4c and 5b) were also used to determine the relationship between K+Rb influx ( $\text{pmol cm}^{-2} \text{ s}^{-1}$ ) and K+Rb root concentrations ( $\mu\text{mol g}^{-1}$ ). In the context here, K+Rb influx is defined by the slope of the depletion curves through the first 5 hours, where depletion curves represented the sums of K plus Rb concentrations. The rate of influx of K+Rb corresponded to the highest concentrations of K plus Rb in solution.

Root samples were oven-dried, ground, and then  $\frac{1}{2}$  gram samples were extracted in 1 N  $\text{HNO}_3$  and shaken for one hour (Stone and Kzystyniak, 1977). Potassium and Rb were determined by atomic absorption spectroscopy, adding 2% cesium to suppress ionization in samples. Potassium and Rb concentrations in the roots at the end of the study were corrected for the amount of K and Rb absorbed during the depletion experiment, assuming that there was no translocation from the root during the experiment. Influx of K+Rb was then compared to the concentrations of K+Rb in the roots. Regression procedures were used to determine whether the slopes were significant (SAS Institute Inc., 1982a). Rates of K+Rb influx were not affected by the initial, total

concentration of K plus Rb in solution, as determined by correlation coefficients for seed source 1 ( $R=0.01$ ,  $P=0.97$ ); seed source 2 ( $R=0.73$ ,  $P=0.02$ ); and seed source 3 ( $R=-0.11$ ,  $P=.69$ ) (SAS Institute Inc., 1982b).

#### Selectivity of K and Rb by slash pine roots

Selectivity coefficients were calculated from those experiments where both K and Rb were present in solution (Expts. 1, 3a,b,c and 4a,b,c), in order to characterize the selectivity or preference for K or Rb by slash pine roots. The coefficients were computed (Baligar et al., 1979) by:

$$SCI = (K/Rb)_{In} / (K/Rb)_{Soln} \quad [4]$$

where SCI is the selectivity coefficient for ion influx,  $K/Rb_{In}$  is the ratio of the individual depletion curve slopes for K and Rb during the first 5 hours of depletion, and  $K/Rb_{soln}$  is the ratio of the initial K and Rb concentrations at  $t = 0$ . A SCI greater than 1 indicates a preference for K, whereas a value less than 1 indicates a preference for Rb by slash pine roots. Relationships of  $K/Rb_{In}$  and  $K/Rb_{soln}$  were analyzed by the Student t-test, to determine if the slopes were significantly different from 1 (Snedecor and Cochran, 1967).

#### Constant K/Rb Ratio Experiments

A separate experiment to determine selectivity coefficients for K and Rb was also conducted. Seedlings were lifted from the tree nursery (seed source 3), root pruned, and grown in an aerated nutrient solution maintained at a K/Rb

ratio of about 7.5:1, with a total K+Rb concentration of 85  $\mu$ M. The solution was replenished every 2 days. After 6, 8 and 10 weeks, 12 seedlings were harvested from each of three replications.

Needles, stems and roots of the seedlings were analyzed for K and Rb using the same procedures as above. The selectivity coefficients for uptake (SCU) were determined from a relationship similar to Eq. [4]; however,  $K/Rb_{In}$  was now taken as the ratio of the amounts of K and Rb absorbed ( $K/Rb_{uptake}$ ) between the sixth and eighth or the sixth and tenth weeks. The SCU's were calculated for roots, needles and entire seedlings (roots, stems and needles). SCU's were not calculated for the stem component, because there was a decrease in K content with time.

## Results

### Michaelis-Menten Parameters

Michaelis-Menten parameters describing K and Rb uptake at various concentrations of K and Rb in solution are presented in Table 2-4. Values of  $I_{max}$  were highly variable among experiments, and results were further confounded by seed source differences which were discovered after the experiments had been conducted. Hence, statistical analyses could not be conducted due to the unbalanced nature of the data. Potassium  $I_{max}$  values showed differences as large as two orders of magnitude among experiments. Potassium  $I_{max}$  values were

Table 2-4. Michaelis-Menten parameters for K and Rb uptake by slash pine seedlings over a range of initial K and Rb concentrations.

Initial Solution Concentration		Michaelis-Menten Parameters			
K	Rb	Potassium		Rubidium	
		Imax	Km	Imax	Km
---	μM---	(μmol cm <sup>-2</sup> s <sup>-1</sup> *10 <sup>6</sup> )	---	μM---	(μmol cm <sup>-2</sup> s <sup>-1</sup> *10 <sup>7</sup> )
SEED SOURCE 1					
70	4	12.57±2.05 <sup>a</sup>	80.1±27.6	9.11±5.26	10.2±7.2
70	7	9.61±0.11	43.9± 1.6	4.42±0.50	1.4±0.5
70	11	11.48	38.1	10.78±0.77	4.4±2.1
SEED SOURCE 2					
70	0.2	15.55±1.13	20.6± 8.3	- <sup>b</sup>	-
70	0.4	13.93±2.29	22.8±11.5	-	-
70	1	9.14±1.16	12.5± 5.5	-	-
42	42	1.81±0.39	12.3± 2.6	16.59±1.03	16.7±6.4
SEED SOURCE 3					
140	0	1.72±0.25	28.6±13.7	-	-
70	0	4.20±0.99	23.2± 8.6	-	-
70	6	0.92±0.10	5.3± 0.6	0.72±0.07	0.0±0.0
70	10	0.90	2.8	1.04±0.11	0.2±0.1
70	70	0.18	11.9	15.60	90.9
35	0	2.68±0.17	1.3±0.4	-	-
30	27	0.87±0.08	22.6±8.7	6.43	4.2
50	5	2.22±0.59	10.6±3.1	1.27±0.16	0.6±0.2
48	8	1.23±0.09	6.9±1.6	2.16±0.28	0.9±0.3

a Average and SE.

b No rubidium present, or only very low amounts.

highest for seed sources 1 and one experiment from seed source 2. Rubidium  $I_{\max}$  values varied by as much as an order of magnitude among experiments, and were highest for seed source 1, and when K and Rb concentrations in solution were similar for experiments using seed sources 2 & 3. Potassium  $I_{\max}$  values were slightly greater than those for Rb with equal concentrations of K and Rb in solution.

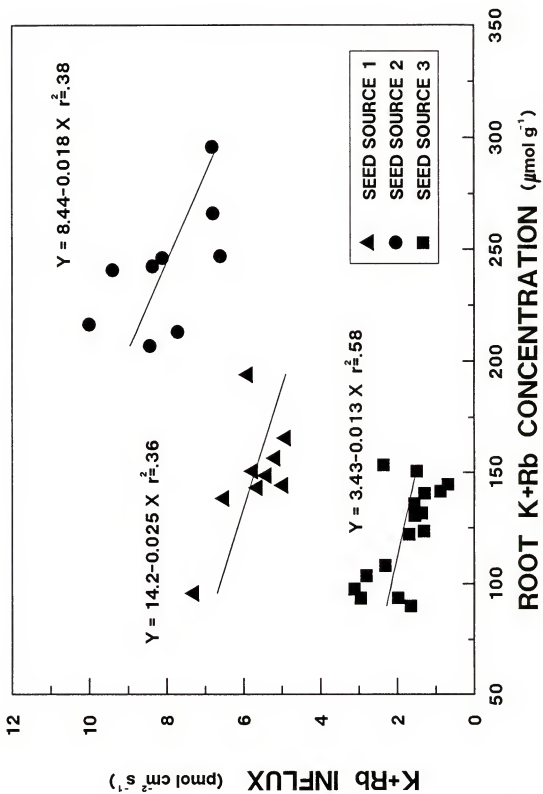
Seedlings from seed source 1, (solution K =  $70\mu\text{M}$ ) showed similar K  $I_{\max}$  values over a range of Rb concentrations ( $0.2$  to  $11\mu\text{mol L}^{-1}$ ). Seedlings from seed source 3, however, exhibited a general decrease in K  $I_{\max}$  values with increasing Rb concentrations, for initial K concentrations of either 30, 50 or  $70\mu\text{M}$ . For solutions with similar initial K concentrations, Rb  $I_{\max}$  values increased with increasing Rb concentration in solution for only seed source 3.

The  $K_m$  values for neither K nor Rb followed any pattern with varying K and Rb concentrations in solution (Table 2-4). Potassium  $K_m$  values were generally 10 times greater than  $K_m$  values for Rb.

#### Ion Influx and Tissue Concentrations

The sum of K and Rb influxes by slash pine roots were found to decrease with increasing root concentrations of K and Rb among experiments (Fig. 2-2). Influxes for seedlings from seed sources 1 & 2 were higher than those for seed source 3 (as discussed previously); however, no significant relationship was found between influx and root concentration

Figure 2-2. Relationship between the initial influx of K plus Rb and the concentration of K plus Rb in the root at the beginning of the experiment, for each of the seed sources.



for seed sources 1 ( $P=0.08$ ) and 2 ( $P=0.09$ ). The relationship between influx and root concentration was significant for seedlings of seed source 3 ( $P=0.01$ ). Correlations of K+Rb influx and needle K+Rb concentrations were not significant for the seed sources.

#### Selectivity of K and Rb by slash pine roots

##### Depletion experiments

The ability of slash pine seedlings to selectively absorb K and Rb was found to vary among seed sources (Fig. 2-3). Seedlings from seed sources 2 and 3 showed no selectivity for K or Rb during absorption experiments (Table 2-5). Seedlings from seed source 1 preferentially absorbed K over Rb by a factor of two (Table 2-5). For all seed sources combined, no selectivity (slope=1.07,  $P=0.05$ ) was observed up to a K/Rb ratio of 10 in solution; including solution ratios up to 12.5, however, resulted in a slight selectivity of K over Rb (slope=1.11,  $P=0.05$ ). Although the SCI for seed sources 2 and 3 indicated no preferential absorption, Rb influx was slightly favoured over K influx at equal concentrations of K and Rb ( $K/Rb_{\text{soln}} \approx 1$ ) as seen by the scatter of points below the 1:1 line (Fig 2-3, inset).

##### Experiments with constant K/Rb ratio

The selectivity coefficient for uptake (SCU) for whole seedlings (seed source 3) was not significantly different from 1 at either 8 or 10 weeks (Table 2-6), which was consistent with the results for seed source 3 using the depletion

Figure 2-3. Relationship between the initial K/Rb influx of slash pine roots and the initial K/Rb solution concentration. Points above the x=y line represent a preference for K by the roots while values below the line indicate a preference for Rb. The inset graph shows influxes below a K/Rb ratio of 2 in solution.

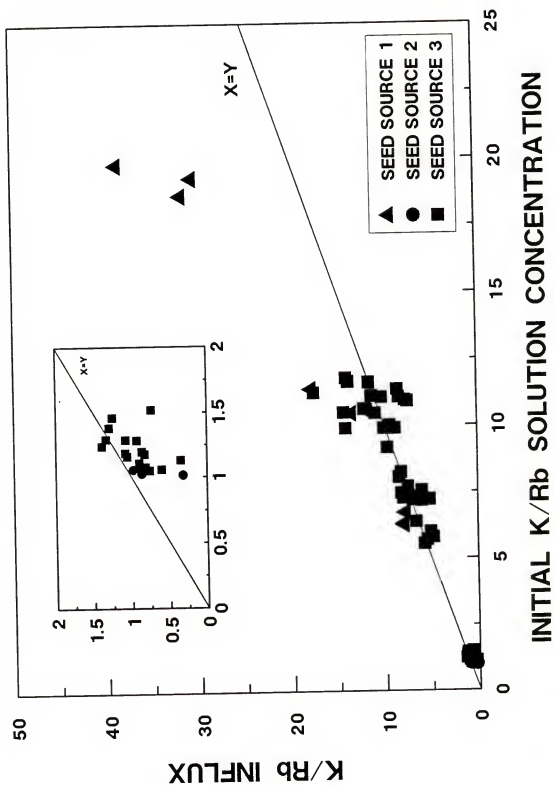


Table 2-5. Selectivity coefficients for influx based on regressions of K/Rb influx vs K/Rb concentrations in solution.

Seed Source	Slope (SCI)	Intercept	$r^2$
1	2.06±0.16 *	-6.43±2.54 *	.96
2,3	1.06±0.05 ns	-0.43±1.56 ns	.89

\* Slope and intercept significantly different from 1 and 0, respectively, at P=0.05.

ns Slope and intercept not significantly different from 1 and 0, respectively at P=0.05.

Table 2-6. Selectivity coefficients for uptake (SCU) by seedling tissues (seed source 3) between 6 and 8 or 10 weeks in a nutrient solution maintained at a constant K/Rb ratio of 7.5.

Time	Tissue	Uptake			SCU
		K	Rb	K/Rb	$\frac{K/Rb_{\text{uptake}}}{K/Rb_{\text{soln}}}$
weeks		----- $\mu\text{mol}$ -----			
6-8	Total <sup>a</sup>	788 $\pm$ 163 <sup>b</sup>	52.7 $\pm$ 14.7	18.7 $\pm$ 6.5	2.49 $\pm$ 0.86
	Needle	389 $\pm$ 109	16.7 $\pm$ 6.1	37.1 $\pm$ 17.7	4.95 $\pm$ 2.37
	Roots	351 $\pm$ 146	23.5 $\pm$ 6.4	15.5 $\pm$ 2.0	2.06 $\pm$ 0.27*
6-10	Total	948 $\pm$ 141	85.5 $\pm$ 10.9	11.1 $\pm$ 1.3	1.49 $\pm$ 0.18
	Needle	422 $\pm$ 16	29.9 $\pm$ 3.6	14.7 $\pm$ 1.8	1.97 $\pm$ 0.25*
	Roots	490 $\pm$ 92	34.9 $\pm$ 5.0	13.7 $\pm$ 0.9	1.83 $\pm$ 0.12*

a Includes needles, stems and roots.

b Average and SE (n=3).

\* Significantly different from 1 at P=0.05.

experiments. Roots at 8 and 10 weeks and needles at 10 weeks, however, accumulated approximately twice as much K than Rb compared to the ratio present in solution. These SCUs were significantly different from 1 ( $P=0.05$ ).

### Discussion

#### K/Rb Selectivity

Plant roots are capable of selectively absorbing ions from external solutions (Epstein, 1972; Marschner, 1986). The proposed mechanism for selectivity involves the competition of the two ions for the same carrier site (Lauchli and Epstein, 1970; Epstein and Hagan, 1952).

A review of selectivity coefficients for K/Rb uptake ( $K/Rb_{\text{uptake}}$ ) and K/Rb influx ( $K/Rb_{\text{in}}$ ) by various plant species showed that a majority of the plant species exhibited a slight preference for K over Rb (Table 2-7). Whether the coefficients were significantly different from 1 is uncertain. Although details of the experiments are not listed here, Marschner and Schimansky (1971) have shown, however, that the degree of selectivity can be affected by the length of experiment, the solution temperature, the total concentration of K plus Rb in solution, the ratio of K/Rb in solution, the nutrient status of the plant and the presence of other ions. Although only one seed source (1) of slash pine had SCI's greater than 1, Schimansky and Marschner (1971) have also

Table 2-7. K/Rb selectivity coefficients for various plant species. Selectivity expressed as a ratio of uptake (SCU) or influx (SCI) by the root to the K/Rb ratio in solution. SCU and SCI values are for the entire plant, unless otherwise specified.

Species	Selectivity Coefficient	Reference
-- SCU --		
Cotton	1.05	Hafez & Raines 1972
Barley	0.93	
Corn	0.95-1.20	Baligar et al. 1979
Onion	1.41-1.73	
Wheat	0.99-1.13	
Onion	1.75-2.20	Baligar & Barber 1978a
Millet	1.10-1.32	Menzel & Heald 1955
Oats	1.11	
Buckwheat	1.18	
Sweet Clover	1.20	
Sunflower	1.15	
Rice	1.00-1.03	
Barley <sup>a</sup> shoot	0.68-3.24	Marschner & Schimansky 1971
root	0.77-2.03	
Barley <sup>b</sup> shoot	0.88-1.18	
root	1.05-1.59	
Barley <sup>c</sup> shoot	1.66-2.03	Schimansky & Marschner 1971
root	1.30-1.73	
Corn shoot	0.97-1.23	
root	0.94-1.02	
Sugar shoot	0.91-1.06	
Beet root	0.92-0.97	
Slash total	1.49-2.49	This study
Pine shoot	1.97-4.95	
root	1.83-2.06	

Table 2-7. Continued.

Species	Selectivity Coefficient	Reference
-- SCI --		
Corn	0.88-1.36	Baligar et al. 1979
Onion	0.91-1.29	
Wheat	1.25-1.33	
Slash	2.06 <sup>d</sup>	This study
Pine	1.06 <sup>e</sup>	

a "High-salt" plants.

b "Low-salt" plants.

c Range is for four varieties of barley.

d Seed source 1

e Seed source 2 & 3.

shown significant differences in selectivities among four varieties of barley.

The preferential absorption of K over Rb suggests that, for most plant species, Rb may not be a satisfactory tracer for K when evaluating uptake on an individual or whole-plant basis. This conclusion is supported by research where Rb was evaluated as a tracer for K in marine algae (West and Pitman, 1967), bean plants (Cline and Hungate, 1960), tomato (Maynard and Baker, 1965), barley (Epstein and Hagan, 1952; Franklin and Snyder, 1965; Behl and Jeschke, 1982) and corn (Mackie and Fried, 1955; Maas and Leggett, 1968). The ratios for K/Rb have also been found to vary among plant tissues (Menzel and Heald, 1955; Cline and Hungate, 1960; Hafez and Raines, 1972; Kszystyniak, 1979), suggesting that discrimination is more likely to occur during the translocation of ions within the plant. Therefore, selectivity coefficients need to be evaluated to determine the validity of using Rb as a tracer for K in plant studies. If preferential absorption exists, then correction factors would be necessary to correct K/Rb ratios; otherwise, results may be misleading. The use of K/Rb ratios for vegetation to infer K/Rb ratios in soil (i.e., in solution or on exchange sites) (Baligar and Barber, 1978b; Baligar, 1985; Buttlemann and Grigal, 1985) is an example of a case where accurate selectivities need to be ascertained.

The Rb/K "reverse tracer technique" of Hafez and Stout (1973) has been used to study the persistence of K in forest

ecosystems (Stone and Kzystyniak, 1977; Stone, 1981; Ohn, 1986). Differences between K/Rb ratios in fertilized and non-fertilized plots are used to estimate K cycling. This technique has been assumed to be valid only when plants do not discriminate in their absorption of K and Rb (Buttleman and Grigal, 1985). Hafez and Stout (1973), however, stated that results would also be valid as long as the fertilized plants selectively absorbed K and Rb in the same manner and to the same extent as non-fertilized plants. Results from this study support both statements, in that trees of one genotype (seed source 1) selectively absorbed K over Rb in the same manner and to the same extent over a range of K/Rb ratios, while another genotype (seed sources 2 & 3) did not discriminate between K and Rb.

#### Comparison of $I_{\max}$ and $K_m$ values

Potassium  $I_{\max}$  values for slash pine, regardless of seed source, were all within the range of  $I_{\max}$  values presented for agronomic crops (Table 2-8). Potassium  $I_{\max}$  values for slash pine (Beck, 1979) were comparable to those for seedlings of seed source 3 on a root volume basis, but were much lower than for seedlings of seed sources 1 & 2 on a unit root volume or unit fresh weight basis. Citrus influxes were much lower than those for slash pine (sources 1, 2 & 3), but other fruit crops such as plum and peach had  $I_{\max}$  values within the range of  $I_{\max}$  values observed for slash pine of seed sources 1 & 2.

Table 2-8. Comparison of potassium  $I_{\max}$  and  $K_m$  values for various plant species grown in solution cultures.  $I_{\max}$  values expressed on a unit root length, surface area, volume, dry weight and fresh weight basis.

Species	Age	K Conc	I <sub>max</sub>	K <sub>m</sub>	Reference
	days	μM		μM	
(μmol cm <sup>-1</sup> s <sup>-1</sup> )*10 <sup>6</sup>					
Corn	20	82-305	1.64-4.97	6-21	Baligar et al. 1979
Corn	10-16	480	1.15-3.61	2.4-3.2	
Onion	15-30	240	3.79-5.21	2.9-28.1	
Wheat	25-35	240	0.50-0.53	3.2-6.9	
Slash Pine	1 yr	70	1.56-4.91 <sup>a</sup> 0.04-0.82 <sup>b</sup>	12-80 2.8-28	This study
(μmol cm <sup>-2</sup> s <sup>-1</sup> )*10 <sup>6</sup>					
Lolium	39	1.2-100	3.34-4.56	15-20	Wild et al. 1979
Raphanus	35	1.2-100	3.67-4.24	15-20	
Soybean		1000	4.6-7.1	4.3-7.1	Peterson & Barber 1981
Slash Pine	1 yr	70	9.6-15.6 <sup>a</sup> 0.87-4.2 <sup>b</sup>	12-80 2.8-28	This study
(μmol cm <sup>-3</sup> s <sup>-1</sup> )*10 <sup>6</sup>					
Slash Pine	1.5 yr	100	48-155	2-143	Beck 1979
Slash Pine	1 yr	70	380-1254 <sup>a</sup> 9-170 <sup>b</sup>	12-80 2.8-28	This study
(μmol g <sub>DWT</sub> <sup>-1</sup> s <sup>-1</sup> )*10 <sup>3</sup>					
Citrus	120	6-50	0.007-0.057	3±1.7	Hassan & Van Hai 1976
Slash Pine	1 yr	70	0.96-4.83 <sup>a</sup> 0.03-0.75 <sup>b</sup>	12-80 2.8-28	This study

Table 2-8. Continued.

Species	Age	K Conc	$I_{max}$	$K_m$	Reference
	days	$\mu M$		$\mu M$	
			$(\mu mol\ g_{FWT}^{-1} s^{-1}) * 10^3$		
Corn	28	100	0.33-1.17	12-70	Beck 1979
Corn	17	1000	1.49-3.66	5-17.5	Claassen & Barber 1977
Prunus	1 yr	100	0.24-0.26	8-10	Rosen &
Plum			0.30	9	Carlson 1984
Peach			0.38	11	
Slash Pine	1 yr	100	0.07-0.08	7-40.8	Beck 1979
Slash Pine	1 yr	70	0.24-1.12 <sup>a</sup>	12-80	This study

a Seed sources 1 &amp; 2.

b Seed source 3.

The difference in K absorption among seed sources suggests that ion uptake may also be controlled by the genetic heritage of the tree. Even though the experiments were conducted over a period of 3 years, differences in air and solution temperatures during the depletion experiments, in seedling size and in K tissue concentrations between the seed sources, did not appear to warrant the 3- to 4-fold difference in rates of uptake. Nielsen and Barber (1978), using 12 corn genotypes, found that  $I_{\max}$  values for phosphorus absorption ranged from 0.12 to 0.40  $\mu\text{mol cm}^{-1}\text{s}^{-1}$ , a 3-fold difference.

#### $I_{\max}$ vs Tissue Concentrations

Potassium influxes have been shown to be negatively correlated with the internal K concentration in roots of barley (Glass, 1976) and in roots of woody perennials such as birch, Norway spruce and Scots pine (Jensen and Pettersson, 1978). Slash pine seedlings from all seed sources appeared to have a slight decrease in  $I_{\max}$  with increasing root concentrations; this relationship, however, was significant only for seed source 3. Although correlations were not very high, the effect of internal K concentrations on uptake suggests the use of the modified Michaelis-Menten equation (Siddiqi and Glass, 1982), which incorporates both external and internal ion concentrations. This type of feedback mechanism approach may prove beneficial for modeling K uptake over long time periods.

### Importance of Uptake Kinetics Under Field Conditions

The ability of certain tree genotypes to acquire more nutrients than others does not necessarily imply that the genotype in question has a more efficient mechanism for ion absorption, and therefore a nutritional advantage when grown in the field. Increased nutrient acquisition can also result from increased root growth rates or from a more finely branched root system; hence, greater root surface area would be present to more effectively exploit the soil. Nye (1977) suggested that the uptake of N, P and K by plants is not limited by the kinetics of absorption, but instead by the processes of diffusion and mass flow that supply nutrients from the bulk soil to the root surface. This fact would appear to be especially true for slash pine growing in the southeastern coastal plain, since these soils exhibit low nutrient concentrations in the soil solution, and small buffer powers as well as poor water-holding characteristics (Chapter 5). Therefore, trees with a higher capacity for nutrient absorption per unit root would provide little advantage on these soils, except under conditions where nutrient supply is not rate-limiting. Hence, tree roots with lower absorption capacities could adequately absorb nutrients under these conditions.

The large range in  $I_{\max}$  values found in this study does not appear to be significant for trees growing under field conditions on these soils. Sensitivity analysis of K uptake

in model simulations for slash pine seedlings grown on a flatwoods Spodosol showed that changing  $I_{\max}$  values 10-fold (change from 0.25 to 2 times the initial value) resulted in less than a 6% change in total K uptake (Van Rees et al., 1989). Therefore, differences in K influxes which are exhibited in controlled solution experiments may not translate into significant increases in total uptake in the field. This conclusion, however, applies only to Spodosols of low K-supplying potential, and generalization to other soil conditions (i.e., fertilized sites) requires further mechanistic evaluations.

### Conclusions

Potassium and Rb influxes showed a slight negative relationship ( $r^2=0.58$ , seed source 3) with K plus Rb concentrations of the roots, supporting a possible feedback mechanism for uptake of these elements by slash pine.

Although a majority of the literature indicates that K and Rb are selectively absorbed by plants, slash pine seedlings from seed sources 2 & 3 exhibited no discrimination, while the opposite was true for seed source 1. Therefore, the use of Rb as a tracer for K should be approached with caution, to avoid misleading results in K cycling or nutrient uptake studies.

Michaelis-Menten parameters used to describe K uptake kinetics for slash pine seedlings in nutrient cultures also

varied among seed sources.  $I_{\max}$  values varied from 0.18 to 15.55  $\text{pmol cm}^{-2} \text{ s}^{-1}$ , and were within the range of values reported for most agronomic crops and for some fruit trees. The wide range in  $I_{\max}$  values may not be important in field situations, however, especially for soils of low K-supplying potential, since diffusion and mass flow have been suggested as the rate-limiting steps in nutrient uptake under such situations.

CHAPTER 3  
THE ROLE OF WOODY ROOTS OF SLASH PINE SEEDLINGS  
IN WATER AND POTASSIUM ABSORPTION

Introduction

Slash pine (*Pinus elliottii* Engelm. var. *elliottii*) roots include newly-formed, unsubsized root tips less than 1 mm in diameter to older subsized roots more than 30 cm in diameter (Koch, 1974; Pritchett and Lyford, 1977). In addition, pine roots can also be modified through their symbiotic association with ectomycorrhizal fungi (Harley, 1978). The diversity in root morphology displayed by slash pine should have a direct effect on root function - particularly with respect to water and nutrient uptake.

Early researchers assumed that the absorption of nutrients and water was restricted to the region of the unsubsized root tip and root hair zones (Scott and Priestley, 1928; Rogers, 1939). Kramer and Bullock (1966), Head (1967) and Wilson and Atkinson (1978), however, have observed that root systems of field-grown trees contain very few growing root tips during periods of high transpiration, suggesting that water absorption must occur through woody roots.

Field-grown tree root systems are predominantly composed of woody roots, so it is appropriate to ask how effective these roots are for water and nutrient uptake. Through the

early work of Crider (1933) and Nightingale (1935) and the more recent experiments of Chung and Kramer (1975) and Atkinson and Wilson (1980), there has been increasing support for the hypothesis that woody roots are an effective surface for water and nutrient absorption. If this hypothesis is true, that woody roots are able to absorb significant quantities of water and nutrients, then it should be possible to evaluate the importance of woody roots on uptake in mechanistic nutrient uptake models.

The purpose, therefore, of this study was to (i) determine the rates of water, potassium (K) and rubidium (Rb) absorption by intact, woody roots of young slash pine seedlings in solution cultures and to contrast such results with those for intact, entire (i.e., woody plus newly-grown roots) root systems; (ii) estimate the quantities of woody and white root length on slash pine seedlings grown under various soil conditions; and (iii) use the results from (i) and (ii), to estimate the relative contributions of woody and white roots for K uptake via a mechanistic nutrient uptake model using soil-grown seedlings.

### Materials and Methods

#### Seedling Collection and Conditioning Prior to Solution Culture Experiments

Fifty 1-year old slash pine seedlings were harvested from a commercial tree nursery in Archer, Florida, root-pruned, and transferred to a 35 L tank containing an aerated, dilute

nutrient solution at pH 4.5 (Table 3-1). Captan was mixed into the nutrient solution on the first day. Seedlings were removed the next day, thoroughly washed with tap water, and transferred to a new nutrient solution. The nutrient solution was replenished every four days during the six-week period of seedling root growth. Root initiation began sometime after the first week in solution. This procedure was repeated prior to the start of each experiment conducted in January, February and June of 1986 and in February of 1987. Seedlings for experiments in 1986 were from seed source 2 (seed collected during 1984 in Florida; general collection), while seedlings for experiments in 1987 were from seed source 3 (seed collected during 1984 in Alabama; high-growth and high-rust resistance clones). Seedlings for the June experiment were harvested in March and cold-stored for one month prior to transferring to the nutrient solution.

The morphology (adhering to the terminology of Sutton and Tinus, 1983) of the newly-grown (non-woody) roots consisted of two forms: white roots located in the region of the root tips and brown-colored roots located behind the white root zones. Whether the newly-grown roots were brown as a result of suberin deposition or of degeneration of epidermis and cortex tissues was not determined. Roots of seedlings obtained from the nursery were classified as woody.

Several days prior to each experiment, all new roots were excised from one half of the seedlings. These seedlings

Table 3-1. Concentrations of ions in the pH 4.5 nutrient solution.

Element	Concentration	Element	Concentration
	---- $\mu\text{M}$ ----		---- $\mu\text{M}$ ----
Nitrate-N	90	Borate-B	0.24
Potassium	77	Iron	0.20
Calcium	75	Rubidium	0.12
Ammonium-N	20	Manganese	0.02
Phosphate-P	20	Zinc	0.02
Magnesium	10	Molybdate-Mo	0.005
Sulphate-S	10	Copper	0.005

developed callous tissue at the cut ends prior to experimentation. Forty-eight hours prior to each depletion experiment, all seedlings were transferred to a nutrient solution lacking K and Rb.

#### Depletion Experiments in Solution Culture

Depletion experiments included two treatments: entire root system left intact (woody roots plus newly-grown roots); and all new root growth excised leaving just the original woody roots. Each treatment consisted of five seedlings in a 2 L plexiglass pot containing 1 to 1.4 L of the aerated nutrient solution, replicated three times. The January experiment was only replicated twice. The tops and sides of each pot were covered to reduce evaporation and shield the roots from light. Marriotte flasks filled with distilled water were connected to each pot to maintain a constant solution volume. The initial K and Rb concentrations for each experiment, as well as the greenhouse environmental conditions, are presented in Table 3-2. Rubidium was measured only in the June 1986 experiment in conjunction with K.

Potassium and Rb concentrations in solution were measured hourly to determine their depletion in solution (Claassen and Barber, 1974). Water uptake by seedlings was measured at similar intervals by recording the loss of water from the marriotte flasks. In the Jan., Feb. and June experiments of 1986, water and nutrient measurements were conducted for 10

Table 3-2. Initial K and Rb concentrations in solution, solution temperatures, and greenhouse conditions for each experiment.

Expt	Initial Soln Conc		Soln Min	Temp Max	Air Min	Temp Max	Light <sup>a</sup>
	K	Rb					
	--- $\mu\text{M}$ ---		----- $^{\circ}\text{C}$ -----		-----		$\mu\text{mol s}^{-1}\text{m}^{-2}$
Jan 86	77	0.12	21	23	25	27	$\text{---}_b\text{---}$
Feb 86	77	0.01	23	25	27	37	1200
June 86	40	40	24	29	28	35	600
Feb 87	77	0	19	25	25	26	1600

a Recorded at 1400 hr

b Not measured.

hours whereas, in the February 1987 experiment, measurements were extended through the night and into the next day.

As part of the February 1987 experiment, several white root tips from seedlings having entire root systems were sealed in mini-containers, internal to the plexiglass pots, in order to separately measure K uptake by the white roots.

In initial studies after the depletion experiments had been conducted, seedling roots were soaked in a 2°C nutrient solution lacking K and Rb. Concentration of K in these solutions after 30 minutes was used to estimate ion mass in the free space of roots. Negligible amounts of K, however, were detected in these solutions with respect to total K uptake; hence, the amount of K in the free space of roots was ignored for total uptake calculations in subsequent work.

#### Growth of Seedling Shoots

In order to index current growth of seedlings in each solution culture experiment, needles of any current flush were collected and weighed.

#### Root Lengths of Seedlings Grown in Soil

The proportions of woody and white roots on slash pine seedlings were determined under three soil-grown conditions: 1) a greenhouse experiment; 2) at a field site in the "Gator National Forest" (GNF), 10 km NE of Gainesville, FL; and 3) at the Container Corporation of America tree nursery near Archer, FL.

### Greenhouse study

Seedlings were grown in the greenhouse in soil material collected from the A horizon of a 4-year old (Pomona 1) and a 25-year old (Pomona 2) slash pine plantation at the GNF. The soils from both sites are classified as Pomona fine sand (sandy, siliceous, hyperthermic Ultic Haplaquods). The soils were air-dried, passed through a 2 mm sieve, and 1.5 kg of material was packed into each 3.5 L plastic pot using 12 pots per soil. Bulk densities for Pomona 1 and 2 were 1.42 and 1.47 Mg m<sup>-3</sup>, respectively. Water contents for Pomona 1 and Pomona 2 were maintained at 0.175 and 0.120 (v/v), respectively, via daily additions of double-deionized water.

Slash pine seed (seed source 4; CGA 189-57, high-rust resistant and low-growth clones) were soaked overnight in water and six seeds planted per pot. Pots were thinned to three seedlings 13 days after planting. Seedlings in each soil were harvested from two pots at 38 and 41 days, and from four pots at 55 and 81 days.

### "Gator National Forest" study

Seedlings were grown in a 12\*1.2 m bed, divided into four compartments. The soil at this site was the same as the Pomona 1 of the greenhouse experiment. One month prior to planting, a 2% solution of glyphosate was applied to the bed to remove unwanted vegetation.

Slash pine seeds (seed source 4) were soaked overnight and then planted in flats in the greenhouse. Thirteen days

after sowing, 80 seedlings were transplanted to each compartment in the field (Time 1). Seedlings were watered daily with well water, and soil water contents ranged from 0.24 to 0.30 (v/v) during the study. Six seedlings were harvested from each compartment at 13, 18, 32, 53 and 81 days after sowing in the greenhouse.

A second replication in time (Time 2), of the study described above, was initiated two weeks after the start of the first experiment (Time 1). An additional 40 seedlings were transplanted into each compartment. Six seedlings from this planting were harvested from each compartment at 13, 53 and 81 days after sowing. All seedlings were harvested by carefully excavating roots of each tree in the A horizon.

#### Nursery study

Soil at the tree nursery site was classified as a Millhopper sand (loamy, siliceous, hyperthermic Grossarenic Paleudults). The section of bed (30\*1.2 m) selected for the study was subjected to standard management procedures for the nursery. Seedling beds were first fumigated and then sown (8 rows per bed) with slash pine seeds (seed source 3) to produce 330 seedlings  $\text{m}^{-2}$  of bed. Fertilization consisted of 392 kg  $\text{ha}^{-1}$  of SUL-P0-MAG (22%  $\text{K}_2\text{O}$ , 18%  $\text{MgO}$ , and 22% sulphur) one month prior to planting followed by two applications of 224 kg  $\text{ha}^{-1}$  of 10-10-10 material at 40 and 48 days after planting. Average soil water contents (15 cm depth) ranged from 0.12 to 0.17 (v/v) during seedling growth.

Four replicates of 10 seedlings each were harvested at 8, 15, 22, 29, 36, 43 and 50 days after sowing on 1 May 1987. Seedlings were harvested by removing a cylindrical column (8 cm radius and 30 cm deep) of soil around each replicate of seedlings.

#### Laboratory Analysis

Potassium and Rb concentrations from the depletion experiments were determined by atomic absorption spectroscopy with 2% cesium to suppress ionization.

Root lengths of seedlings growing in both the solution and soil environments were measured by the line-intercept method of Newman (1966). Root surface area was calculated using the total root length and an average weighted root radius. Root radius ( $r_o$ ) was calculated for the taproot, woody and newly-grown roots by:

$$r_o = [F_{wr}/\pi L]^{\frac{1}{2}} \quad [1]$$

where  $F_{wr}$  is fresh root weight and  $L$  is total root length. This equation assumes a root density of  $1 \text{ Mg m}^{-3}$ . Woody and white root lengths for seedlings grown in soil are expressed as average root length per seedling.

Rates of uptake for water, K and Rb are expressed as total uptake per time on a pot, unit root length, and unit root surface area basis. A net negative uptake for K indicates that efflux was greater than influx during the study.

Differences in water, K and Rb uptake between entire and woody root systems were tested by the Student t-test at the  $P=0.05$  level for each experiment.

Evaluation of K Uptake by Woody and White Roots with a Mechanistic Model

Predictions of K uptake for woody and white roots were contrasted with K uptake for entire root systems via the Barber-Cushman model (BCM), using data from seedlings grown in the greenhouse and at the tree nursery. Briefly, the soil parameters used in the simulations include the initial concentration of K in soil solution ( $C_{11}$ ); the soil buffer power ( $b'$ ); the effective diffusion coefficient ( $D_e$ ) of K in the soil; and the average water influx ( $V_o$ ). The plant parameters include root radius ( $r_o$ ); mean half-distance between roots ( $r_1$ ); initial root length; root growth rate ( $k$ ); and the Michaelis-Menten parameters that describe ion influx at the root surface -  $I_{max}$ ,  $K_m$ , and  $C_{min}$ . The estimation of these parameters is discussed in detail in Chapter 5 and a complete list of parameter values for each simulations is found in Appendix A.

Ranges in parameter estimates used in the K uptake simulations for entire root systems and woody and white roots are presented in Table 3-3. The soil parameters and plant parameters -  $r_1$ ,  $r_o$  and  $C_{min}$  used in K uptake predictions for the entire root system were also used for uptake simulations for woody plus white roots and for white roots alone. Root growth rates, initial root lengths and Michaelis-Menten

Table 3-3. Range in soil and plant input parameters for K uptake predictions for seedlings grown in the greenhouse (Pomona 1 and Pomona 2) and at the tree nursery. All soil parameters,  $r_1$ ,  $r_o$  and  $C_{min}$  were used for K uptake for entire root systems, woody roots and white roots.

Parameter	Greenhouse Study		Nursery Study
	Pomona 1	Pomona 2	
----- Soil Parameters -----			
$D_o$ ( $\text{cm}^2 \text{s}^{-1}$ ) $\times 10^{-7}$	0.99-1.04	0.20-0.26	0.21-0.68
$b'$	3.64	6.11	6.26
$C_{11}$ ( $\mu\text{mol cm}^{-3}$ )	0.136	0.093	0.203
$V_o$ ( $\text{cm s}^{-1}$ ) $\times 10^{-6}$	2.23-4.07	2.26-10.35	3.79
----- Plant Parameters -----			
$r_1$ (cm)	0.84-1.54	0.62-2.02	0.75-2.59
$r_o$ (cm)	0.038-0.042	0.036-0.043	0.027-0.046
$C_{min}$ ( $\mu\text{mol cm}^{-3}$ )	0.001	0.001	0.001
Time (days)	0-81	0-81	0-50
Entire Root System			
$L_o$ (cm)	11.9	11.9	41.3
$k$ ( $\text{cm s}^{-1}$ ) $\times 10^{-4}$	1.16-1.97	0.64-2.64	0.86-4.55
$I_{max}^a$	3.61	3.61	3.61
$K_m$ ( $\mu\text{mol cm}^{-3}$ )	0.029	0.029	0.029
Woody Root Component			
$L_o$ (cm)	5.0	5.0	20.63
$k$ ( $\text{cm s}^{-1}$ ) $\times 10^{-4}$	0.70-1.67	0.45-2.37	0.72-3.25
$I_{max}^a$	2.33	2.33	2.33
$K_m$ ( $\mu\text{mol cm}^{-3}$ )	0.0042	0.0042	0.0042
White Root Component			
$L_o$ (cm)	6.85	6.85	20.63
$k$ ( $\text{cm s}^{-1}$ ) $\times 10^{-5}$	0.24-0.49	0.14-0.38	1.4-8.69
$I_{max}^a$	2.96	2.96	2.96
$K_m$ ( $\mu\text{mol cm}^{-3}$ )	0.010	0.010	0.010
a Units are ( $\mu\text{mol cm}^{-2} \text{s}^{-1}$ ) $\times 10^{-6}$ .			

parameters ( $I_{\max}$  and  $K_m$ ), however, were calculated separately for each of the woody and white root components (Table 3-3). The Michaelis-Menten parameters (absorption assumed to be an active process for both root types) were determined using the depletion technique (see Chapter 2) for seedlings of the February, 1987 experiment.

Predicted K uptake by the sum of woody plus white roots was plotted against predicted K uptake for the entire root system. Simulations of K uptake by white roots alone (i.e., no K absorption by woody roots) were also plotted against the results for entire root systems. Student t-tests were used to determine if slopes were significantly different from one at  $P=0.05$ .

## Results

### Evidence of Seedling Growth in Solution Cultures

Seedlings in the January and February experiments of 1986 did not have any current flushes of new growth. New flushes of growth, however, were observed for seedlings in the June, 1986 and February, 1987 experiments (Table 3-4).

### Water Uptake

Seedlings with entire root systems had greater root lengths (5.6 to 6.3 times) and root surface areas (2.1 to 4.7 times) than those seedlings with just woody roots (Table 3-4). These differences resulted in a significant increase (2.5 to 4.2 times) in water absorption per pot for the entire

Table 3-4. Seedling shoot weights, root length and root surface areas for the different root treatments. Values are means and SE estimates per pot for seedlings with entire root systems and for woody and white roots.

Expt.	Shoot Dry Weight		Root Length		Root Surface Area	
	Entire	Woody	Entire	Woody	Entire	Woody
	----- g -----		----- m -----		----- m <sup>2</sup> *10 <sup>3</sup> -----	White
Jan 86	12.7±1.4	9.9±0.6	35.54±2.65	5.60±0.25	89.7±11.3	18.5±0.8
Feb 86	18.0±1.2	17.3±0.6	29.38±2.16	4.76±0.57	78.7± 5.0	20.6±2.5
June 86	21.2±0.9 (3.2±0.6) <sup>b</sup>	17.8±1.2 (3.0±0.5)	24.97±0.58	4.37±0.22	51.2± 1.8	24.4±1.1
Feb 87	8.4±0.5 (0.7±0.1)	13.7±0.4 <sup>c</sup> (1.4±0.1) <sup>c</sup>	23.65±1.66	4.25±0.23	48.8± 6.9	18.8±0.7
						2.7±0.1

a Where measured, refers to white roots sealed in mini-container.

b ( ) represents dry weights of active flush of growth.

c Values are weights after the seedlings had been used in another experiment, 1 month later.

root system with respect to woody roots (Fig. 3-1a). Water absorption by woody roots expressed on a unit root length basis, however, was comparable (June 1986 and Feb. 1987) or significantly greater (Jan. and Feb. 1986) than that for the entire root system (Fig. 3-1b). Per unit root surface area, woody roots for the January experiment had much higher rates, whereas the two February experiments were comparable to entire root systems (Fig. 3-1c). Entire root systems absorbed significantly more water than woody roots, per unit root surface area, in the June experiment only. Similar results were found for water absorption by entire and woody root systems during day and night hours (Appendix B). Therefore, under the conditions described here, woody roots are functional in water uptake, and are often comparable to entire root systems when uptake is expressed per unit of root.

#### Potassium and Rubidium Uptake

In the Jan. and Feb. experiments, entire root systems of slash pine absorbed significantly more K than woody root systems, regardless of the unit of measurement (Fig. 3-2a,b,c). Net K absorption by woody roots was small or even negative (i.e. net efflux) in these two experiments, coinciding with no new shoot growth for the seedlings.

In the June experiment, with equal initial solution concentrations of K and Rb, K uptake by complete and woody root systems was comparable with respect to all three units of measurements although net K uptake was much lower than in

Figure 3-1. Water uptake by woody and entire (woody plus newly-grown roots) root systems of slash pine seedlings from solution cultures. Water uptake is expressed per pot (a), per unit root length (b) and per unit root surface area (c). Error bars are SE of the means and "\*" indicates significant differences in water absorption between root treatments (within each experiment) at  $P=0.05$ .

## WATER UPTAKE

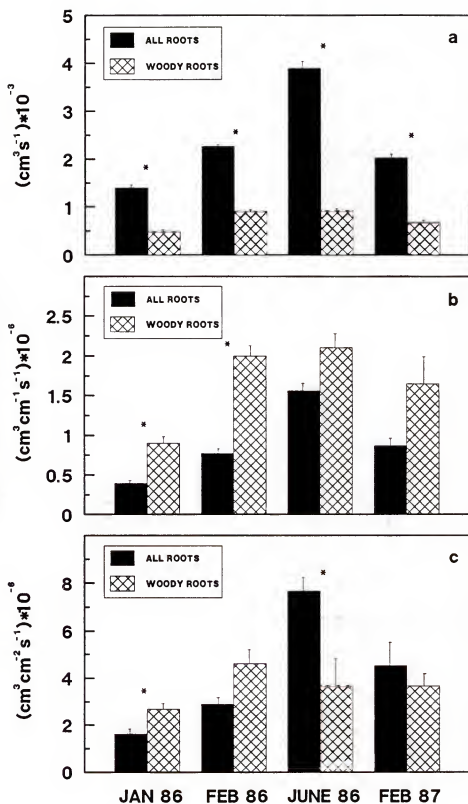
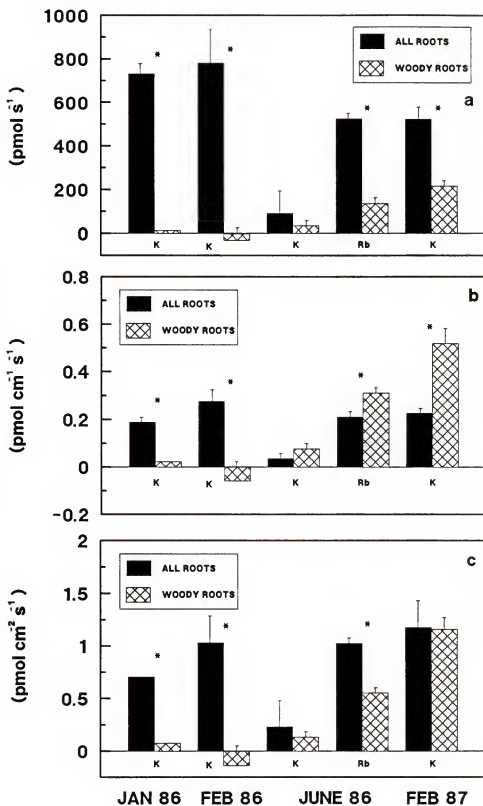


Figure 3-2. Potassium (K) and rubidium (Rb) uptake by woody and entire (woody plus newly-grown roots) root systems of slash pine seedlings in solution cultures. Uptake is expressed per pot (a), per unit root length (b) and per unit root surface area (c). Error bars are SE of the means and "\*" indicates significant differences in K or Rb absorption between root treatments (within each experiment) at  $P=0.05$ .

## K and Rb UPTAKE



the other experiments. In contrast, entire root systems absorbed significantly more Rb than woody roots on both a pot and root surface area basis (Fig 3-2a,c). The reverse was true on a root length basis, where Rb uptake by woody roots was larger (Fig. 3-2b).

For the February, 1987 experiment, K uptake by the entire and woody root systems followed the same trend as the Rb experiment (Fig. 3-2a,b); K uptake by the two root systems, however, was comparable when expressed on a surface area basis (Fig. 3-2c). Absorption of K by white roots sealed in the mini-containers in February, 1987 was  $0.58 \pm 0.14 \text{ pmol cm}^{-1} \text{ s}^{-1}$  and  $1.72 \pm 0.25 \text{ pmol cm}^{-2} \text{ s}^{-1}$ , and neither of these rates were significantly different from uptake by woody roots.

In general, seedlings with entire root systems, that had no active shoot growth, absorbed significantly more K than for woody roots. When shoot growth was active, however, K or Rb uptake per unit root length by woody roots was larger than for entire root systems. Per unit surface area, uptake by woody roots was comparable to or less than entire root systems.

#### Potassium Uptake and Mass Influx

Estimates of mass influx (i.e. water uptake x the average K solution concentration) provide an estimate of the maximum amount of K that the plant could acquire by passive uptake via the transpiration stream. Passive uptake, in this sense, is used to describe uptake through an apoplastic pathway requiring no metabolic energy. Hence, differences between net

K uptake and mass influx give an estimate of the minimum active uptake by the root in solution culture. Mass influx estimates accounted for 7 to 50% of the total K or of the K plus Rb (June expt.) uptake by entire root systems (Fig. 3-3). Seedlings with woody roots and actively growing shoots had mass influx estimates of 26 to 30% of the total K uptake; however, mass influx estimates accounted for all or more of the K uptake in woody roots, where there was no active shoot growth.

#### Root Lengths for Soil-Grown Seedlings

Woody and white root lengths of slash pine seedlings grown in the greenhouse, in the "Gator National Forest" and in the tree nursery are presented in Figure 3-4. In general, root growth rates for seedlings were largest for the greenhouse, followed by the nursery and the field (GNF). Regardless of the environment in which the seedlings were grown, white root length ranged from 5 to 15% of the entire root length at 80 days, and remained fairly constant with time. Rates of development for woody (assuming that woody root length is added by maturation of white roots) and white roots in soil for the three studies ranged from  $(0.95-5.89) \times 10^{-5}$  and  $(1.47-7.94) \times 10^{-6}$  cm s<sup>-1</sup>, respectively.

#### Evaluation of K Uptake by Woody and White Roots using BCM

Predicted values of K uptake by the sum of the woody plus white root component and the entire root system of seedlings grown in the greenhouse and the tree nursery were not

Figure 3-3. Estimated mass influx for woody and entire root systems expressed as a % of the net K uptake for slash pine seedlings grown in solution culture.

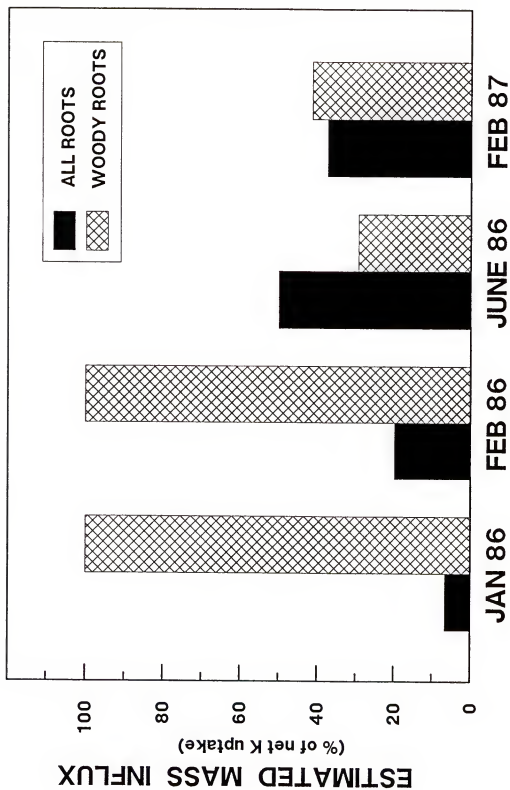
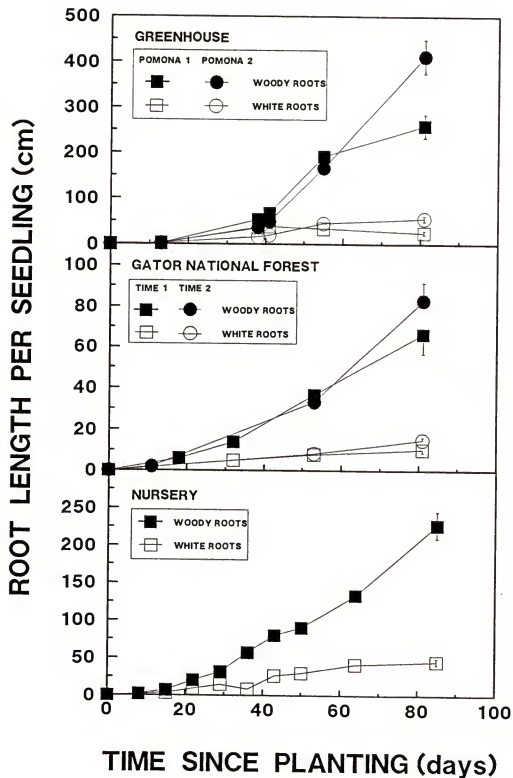


Figure 3-4. Root lengths of slash pine seedlings grown in the greenhouse, the field (Gator National Forest) and a tree nursery. Error bars represent SE of the means.



significantly different from one (slope=1.00,  $r^2=.99$ ) (Fig. 3-5). Potassium uptake simulated for white roots only (i.e., no uptake by woody roots), however, was only 22% ( $r^2=.86$ ) of the total uptake by the entire root system.

### Discussion

#### Water and Nutrient Uptake

Many researchers in plant nutrition have assumed that water and nutrient absorption occurs mainly through white roots (Scott and Priestley, 1928; Pritchett and Lyford, 1977; Persson, 1980). The results from this study, however, indicate that woody roots of slash pine are able to effectively absorb water, K and Rb from nutrient solutions. Moreover, absorption of water, K and Rb per unit of root length for woody roots of seedlings with active shoot growth, was comparable to or better than that for entire root systems.

Rates of water uptake by intact woody roots in this study are also consistent with literature data for other perennial, woody species (Table 3-5). Water uptake by white roots was included in Table 3-5, to emphasize the relative importance of woody roots in water absorption.

Similarly, K and Rb absorption by woody roots of slash pine were comparable to K (using  $^{86}\text{Rb}$ ) uptake rates by cherry on a surface area basis (Table 3-6). Although K and Rb absorption by woody roots cannot be extrapolated to other nutrients, researchers have found that woody roots of some

Figure 3-5. Predicted K uptake by the Barber-Cushman model for the sum of woody plus white roots (open symbols), or white roots alone (filled symbols) and the entire root system. The 1:1 line represents a perfect correlation in K uptake predictions for the entire root system and separate components of the root system (i.e., woody plus white or white alone).

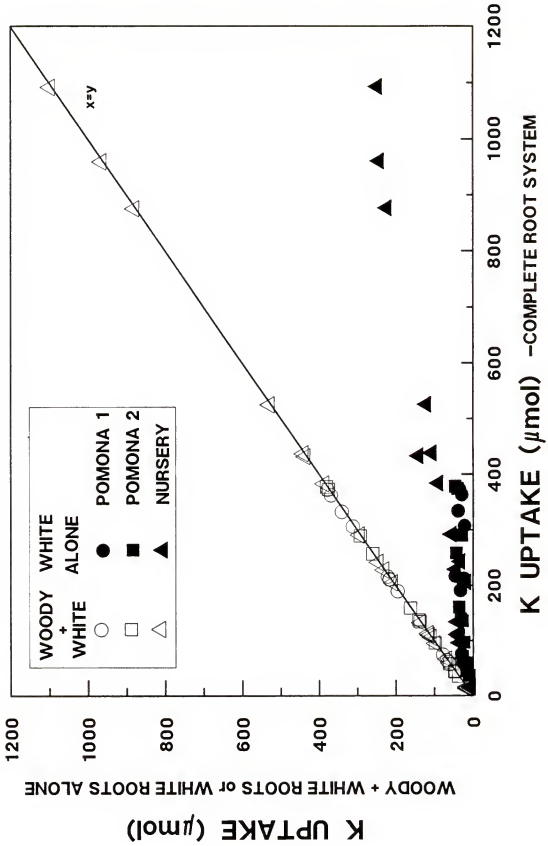


Table 3-5. Summary of water uptake by woody and white roots and entire root systems of perennial woody plants. Uptake for intact roots unless specified otherwise.

Species	Root Type	Root Growing Medium	Water Uptake ( $\text{cm}^3 \text{cm}^{-2} \text{s}^{-1}$ ) * $10^6$	Method	Reference
<u>Pinus taeda</u> (1 yr old)	All	Solution	4.86±0.28 <sup>a</sup>	Pressure <sup>b</sup>	Chung & Kramer 1975
	All	Vermiculite	3.86±0.36		
	All <sup>c</sup>	Solution	3.44±0.17		
	All <sup>d</sup>	Solution	4.28±0.31		
	Woody	Solution	3.61±0.21		
<u>P. taeda</u> <sup>e</sup>	White	Solution	14.19±1.44	Pressure	Kramer & Bullock 1966
	White	Vermiculite	11.53±1.35		
	Woody	Woody	1.53±0.17		
<u>P. taeda</u> <sup>e</sup>	White	Solution	8.5-115.3 (x=49.4)	Pressure	Kramer & Bullock 1966
	White	Solution	3.6-45.3 (x=20.3)		
	White	Soil	1.2-26.9 (x=10.4)		
	Woody	Soil	1.83 (1 mm dia)		
	Woody	Soil	1.19-8.89 (1-2 mm dia)		
	Woody	Soil	22.2 (5 mm dia)		
	Apical	Soil	49.44		
	Mycorr	Soil	49.44		
	Woody	Soil	1.83 (<1.33 mm dia)		
	Woody	Soil	10.17 (>1.33 mm dia)		
<u>P. echinata</u>	Woody	Solution	0.28-2.32 (June)	Potometer	Kramer 1946
	Woody	Solution	0.36-0.58 (Aug.)		

Table 3-5. Continued

Species	Root Type	Root Growing Medium	Water Uptake (cm <sup>3</sup> cm <sup>-2</sup> s <sup>-1</sup> ) * 10 <sup>6</sup>	Method	References
<u>P. echinata</u> <sup>e</sup>	Woody	Solution	2.5	Pressure	Kramer 1946
<u>Cornus</u> <sup>e</sup>	Woody	Solution	4.33		
<u>Liriodendron</u> <sup>e</sup>	Woody	Solution	28.17		
<u>tulipifera</u>					
<u>Prunus</u> (3 month)	Woody White	Solution Solution	3.89±0.28 5.00±1.10	Potometer	Atkinson & Wilson 1979
<u>Citrus</u> (2 yr)	Woody	Solution	0.46-1.39	Potometer	Hayward et al. 1942
<u>P. ellioti</u> (20 months)	Woody White	Soil Soil	1.00±0.20 1.81±0.22	Potometer	Klawitter as reported by Chung & Kramer 1975
<u>P. ellioti</u> (1 yr)	All Woody	Solution Solution	1.62-7.65 2.70-4.62	Marriotte flask	This Study

a Mean and SE.

b Uptake determined by applying vacuum (41 kPa) to one end of a root immersed in water.

c Dormant root system.

d 1/3 of white roots removed.

e Root segments.

Table 3-6. Summary of ion uptake by entire root systems and woody and white root components of perennial woody plants.

Species	Root Type	Ion	Uptake pmol cm <sup>-2</sup> s <sup>-1</sup>	Method	Reference
<u>Prunus</u> (3 months)	Woody	K( <sup>86</sup> Rb)	0.97±0.14 <sup>a</sup>	Potometer	Atkinson & Wilson 1980
	White	K( <sup>86</sup> Rb)	1.69±0.97		
<u>Malus</u>	Woody	<sup>45</sup> Ca	0.83±0		
	White	<sup>45</sup> Ca	2.78±0.28		
<u>Prunus</u> (3 months)	Woody	<sup>45</sup> Ca	1.67±1.39	Potometer	Atkinson & Wilson 1979
	White	<sup>45</sup> Ca	1.94±28		
<u>Pinus taeda</u>	Woody	<sup>32</sup> P	4.39±0.18	Potometer	Atkinson & Wilson 1979
	White	<sup>32</sup> P	5.38±1.26		
<u>P. elliotii</u> (1 yr)	All	<sup>32</sup> P	0.093±0.014 <sup>b</sup>	Pressure	Chung & Kramer 1975
	Woody	<sup>32</sup> P	0.049±0.012		
<u>P. elliotii</u> (1 yr)	All	K	1.18±0.46	Nutrient depletion curves	This study Feb. 1987
	Woody	K	1.16±0.22		
	White	K	1.72±0.25		
	All	Rb	1.03±0.07		June 1986
	Woody	Rb	0.55±0.06		

a Mean and SE.

b Units are c.p.m. cm<sup>-2</sup> s<sup>-1</sup>.

tree species were effective, and in some cases as efficient as, white roots in absorbing  $^{45}\text{Ca}$  and  $^{32}\text{P}$  from solution (Table 3-6).

Caution is necessary, however, when comparing these studies because of differing methodology (pressure vs potometer) and differing types of root sample used (cut root segments vs intact root systems). Intact root systems generally give lower rates of water uptake, which may be attributed to increased resistances along the length of the root system (Newman, 1976).

Most water and nutrient uptake studies are conducted in nutrient solutions; hence, uptake results may not represent those for roots growing in soil. Kramer (1946), however, found that water uptake by intact, woody roots of shortleaf pine was  $0.94 \text{ cm}^3\text{cm}^{-2}\text{s}^{-1}$  when the potometer was filled with water, and  $0.73 \text{ cm}^3\text{cm}^{-2}\text{s}^{-1}$  when the potometer was filled with moist soil. Thus, it would appear that woody roots growing in soil function in absorption, but possibly at lower rates, than roots grown in solution cultures (Chung and Kramer, 1975).

The importance of woody roots to slash pine nutrition under field conditions, however, will depend on the amounts and distribution of these roots in the soil profile. Such factors will vary with tree age and with season of the year. For seven-week old seedlings in this study, the proportion of woody root length exceeded that of white root length.

Therefore, the amount of absorbing root surface area attributed to white roots, during a rotation, could be very small in relation to that of woody roots. Estimates of root surface area calculated from work by Pritchett and Lyford (1977) showed that root tips (mycorrhizal and nonmycorrhizal), assuming an average root length of 1 cm and radii of 0.015 cm, comprised 18% of the total root surface area in a 25-yr old slash pine tree in February. Kramer and Bullock (1966) reported that roots in the surface horizon of a 34-yr old loblolly plantation, during the period from March to November, had less than 1% of the total root surface area in growing root tips. Suberized root surface areas ranged from 99% in March to 93% in May. For young apple trees, Wilson and Atkinson (1978) also estimated that the proportion of brown (suberized and woody) root length ranged from 15 to 100% of the total root length. The large proportion of woody roots on field-grown trees, therefore, suggests that their contribution to uptake can be significant, particularly at certain times of the year.

#### Evaluation of K Uptake by Woody Roots using BCM

In solution cultures, woody roots were shown to be effective in water and nutrient uptake with respect to the entire root system. Simulations of K uptake for the sum of woody and white roots of soil-grown seedlings, however, were no different than uptake for the entire root system. Therefore, under these conditions, K uptake simulations can

be adequately modeled by determining plant parameters for the entire root system, instead of separating the root system into woody and white root components. This does not imply, however, that woody and white roots are not equally important for the acquisition of water and nutrients by trees in the field; indeed the contrary has been discussed above.

Simulations for white roots alone accounted for only 22% of the total K acquired by seedlings with woody plus white roots. Soil processes were found to be the rate-limiting step in K acquisition for these soils (i.e., not plant-limited); therefore, increasing  $I_{\max}$  values for white roots would not significantly increase uptake to the levels predicted by the entire root system (Chapter 5). Although the effect of altering the rates of uptake would not increase uptake predictions, the amount of absorbing woody root surface area is essential for accurately predicting K uptake.

Modeling efforts by Blake and Hoogenboom (1988) and by Protopapas and Bras (1987) have attempted to separate the woody and white root components for water absorption. Blake and Hoogenboom (1988) assigned different radial and axial resistances to suberized and unsuberized roots of loblolly pine, while Protopapas and Bras (1987) assumed that only 30% of the old (suberized) roots were functional in water uptake. Water uptake for the entire root system was described by a weighted value of the effective root conductivity. Results from these models were not validated. Future water and

nutrient modeling efforts, however, should attempt to incorporate measured rates of water and nutrient uptake by woody and white roots.

#### Pathways and Mechanisms for Uptake by Woody Roots

The pathways and mechanisms whereby woody roots absorb water and nutrients are still uncertain. Although estimates of mass influx (i.e. passive uptake) for seedlings with active shoot growth accounted for as much as 50% of the uptake, an active mechanism for uptake may also be occurring within woody roots.

Although this study did not look at the effect of the suberized endodermis on uptake, a review of possible pathways for water and nutrient movement through the endodermis is given by Dumbroff and Peirson (1971), Clarkson and Robards (1975), Clarkson et al. (1978) and Drew (1987). For the soil-root interface, Addoms (1946) suggested that water entry across the periderm occurred through lenticels, around the edges of overlapping periderm plates, around branch roots and through wounds. The parenchymatous cells of lenticels in Citrus have also been suggested as entry points by Hayward et al. (1942). Atkinson and Wilson (1979), however, stated that the low variability in uptake by woody roots suggests that these sites of entry would need to be uniformly distributed on the root surface.

The absorption of solutes by roots has been related to shoot growth, although the relationship is somewhat complex

(Russell and Clarkson, 1971; Sutcliffe, 1986). Woody roots were found to be more effective in K absorption for seedlings with active shoot growth than for those with none, suggesting a link between woody root function and active shoot growth. Seedlings with entire root systems and no shoot growth, however, were still able to absorb K, suggesting that K was absorbed in order to maintain the physiological processes of the actively growing roots.

### Conclusions

Woody roots of slash pine are an effective surface for water absorption and for K or Rb absorption when seedlings have active shoot growth. Woody roots of seedlings grown in solution cultures were as efficient or better in absorbing water, K and Rb than entire root systems when uptake was expressed per unit of root length. The mechanisms whereby woody roots absorb nutrients, however, is still uncertain and deserves further research.

Using separate plant parameters for woody and white roots of slash pine in a mechanistic nutrient uptake model resulted in K uptake predictions similar to those determined for plant parameters measured for the entire root system. The amount of woody roots, however, is essential for accurately predicting K uptake as shown by the underpredictions which resulted when using white root lengths alone.

The effectiveness of woody roots in water and K absorption, in addition to the large proportion they comprise of the total root system, suggests that woody roots can play a major role in the nutrition of slash pine stands.

CHAPTER 4  
DEFINING SOIL BUFFER POWER: IMPLICATIONS FOR  
ION DIFFUSION AND NUTRIENT UPTAKE MODELING

Introduction

The term "buffer power" has frequently been defined in the literature as the total amount of diffusible ion (solution plus sorbed) per unit volume of soil required to increase the solution concentration by 1 unit (Olsen et al., 1965; Nye, 1966a,b; Nye, 1968; Olsen and Kemper, 1968; Vaidyanthan et al., 1968; Claassen and Barber, 1976; Nye and Tinker, 1977; Cushman, 1984). Buffer power, however, has also been described as the relationship between the concentration of ions adsorbed on the solid phase and ions in solution (Barber, 1979; Barber and Cushman, 1981; Silberbush and Barber, 1983, 1984; Silberbush et al., 1983; Barber, 1984; Mullins and Sommers, 1986). Both definitions of buffer power have been used for estimating molecular diffusion coefficients or nutrient replenishment of the soil solution.

One definition of the buffer power is correct for any given condition. Under specific conditions, however, the wrong definition can result in significant errors, especially for plant nutrient uptake models (Nye and Tinker, 1977; Silberbush and Barber, 1983, 1984; Mullins et al., 1986; Rengel, 1988; Chapter 5) where reliable estimates of ion

diffusion and nutrient replenishment of the solution phase are required.

The purpose, therefore, of this note is to 1) define the conditions under which each definition of buffer power is valid, and 2) present situations where improper application of buffer powers could lead to erroneous conclusions.

### Theory

The solute transport equation for one-dimensional, diffusion under steady-state water conditions is:

$$\partial C_T / \partial t = [D_L \theta f] \partial^2 C_L / \partial x^2 \quad [1]$$

where  $C_T$  is the total amount of diffusible ion (solution plus sorbed phases) per unit volume of soil ( $ML^{-3}$ ),  $t$  is time ( $T$ ),  $D_L$  is the molecular diffusion coefficient ( $L^2T^{-1}$ ) in bulk water,  $\theta$  is the volumetric water content ( $L^3L^{-3}$ ), and  $f$  (dimensionless), a function of  $\theta$ , is the impedance factor which accounts for the tortuous pathways in the soil pore sequence (Porter et al., 1960). For most soils,  $f$  values range from 0.3 to 0.7 (van Genuchten and Wierenga, 1986). The ion concentration in soil solution,  $C_L$  ( $ML^{-3}$ ), is taken at a point  $x$  ( $L$ ) in the direction of net ion movement.

The total amount of diffusible ion,  $C_T$ , in a unit volume element can be stated as:

$$C_T = \theta C_L + \rho C_s \quad [2]$$

where  $\rho$  is the bulk density ( $ML^{-3}$ ) and  $C_s$  is the adsorbed amount of diffusible ion ( $MM^{-1}$ ).

Assuming that  $C_s$  and  $C_L$  are related by an instantaneous, reversible, linear adsorption (or desorption) isotherm, then:

$$C_s = K_d C_L \text{ or } K_d = C_s / C_L \quad [3]$$

where  $K_d$  is the slope of the isotherm ( $L^3 M^{-1}$ ). Substituting Eq. [3] into [2] yields:

$$C_T = \theta C_L + \rho K_d C_L = (\theta + \rho K_d) C_L \quad [4]$$

where  $(\theta + \rho K_d)$  would be the slope if  $C_T$  (solution plus sorbed phases) were plotted against  $C_L$ .

Substitution of Eq. [4] in Eq. [1] gives:

$$\partial C_L / \partial t = [D_L \theta f / (\theta + \rho K_d)] \partial^2 C_L / \partial x^2. \quad [5]$$

Based on Eq. [5], the effective diffusion coefficient ( $D_e$ ), can then be defined as:

$$D_e = D_L \theta f / b' \quad [6]$$

where  $b'$ , the soil buffer power, is defined as:

$$b' = (\theta + \rho K_d) = \partial C_T / \partial C_L. \quad [7]$$

Note that rearranging Eq. [6],  $D_e$  can also be defined as:

$$D_e = D_L f / R \quad [8]$$

where  $R$ , the retardation factor (Hashimoto et al., 1964; Davidson and Chang, 1972), is:

$$R = (1 + \rho K_d / \theta) \quad [9]$$

$D_e$  has also been expressed in the literature (Olsen et al., 1962; Barber, 1980, 1984; Barber and Cushman, 1981; Silberbush and Barber, 1983; Silberbush et al., 1983; Mullins and Sommers, 1986) as:

$$D_e = (D_L \theta f / b) \quad [10]$$

where the buffer power ( $b$ ), in this case, is defined as:

$$b = \rho K_d = \rho (\partial C_s / \partial C_L). \quad [11]$$

## Discussion

### Validation of Buffer Power

The ratio between the two forms of buffer power (Eqs. [7] and [11]) can be calculated by:

$$b'/b = 1 + \theta/\rho K_d. \quad [12]$$

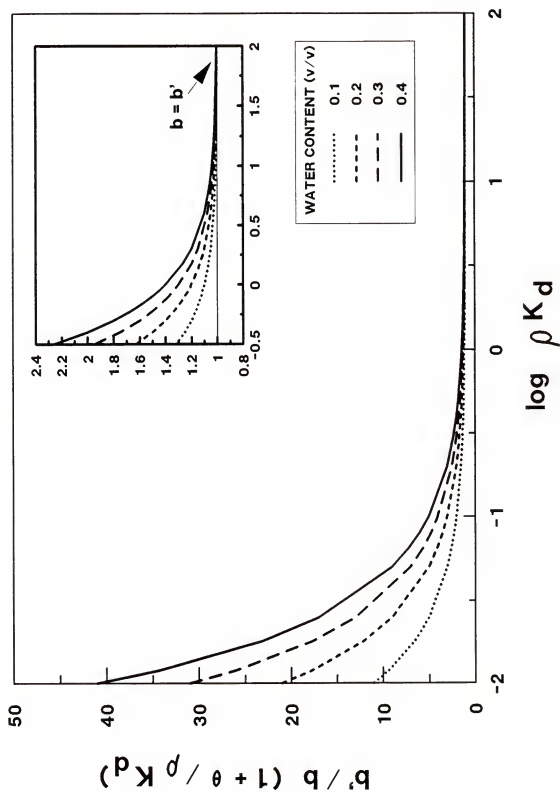
As  $\rho K_d$  gets very large (i.e.,  $\log \rho K_d > 1.5$ ), the contribution of  $\theta$  becomes insignificant and  $b$  approximates  $b'$  (Fig. 4-1). As  $\rho K_d$  approaches 0, however, the difference between the two buffer powers rises exponentially. Therefore, Eq. [11] is only valid for describing soil buffer power when the total amount of diffusible ion on the solid phase is much greater than that in the solution phase (i.e.,  $\rho K_d \gg \theta$ ). However, this assumption is not usually stated.

The value of  $\rho K_d$  that would make Eq. [11] valid also depends on the level of error accepted by the user. For example, a sensitivity analysis of the parameters affecting K uptake for slash pine grown in the field, showed that a 10% change in the buffer power resulted in a 15% error in K uptake predictions (Chapter 5). If one accepts a 15% error in uptake then, under these conditions, Eq. [11] would be satisfactory for calculating buffer power when  $\rho K_d$  is 10 times greater than  $\theta$ , or  $K_d > 10(\theta/\rho)$ . Otherwise, Eq. [6], where  $b' = \theta + \rho K_d$ , should be used.

### Some Specific Problems in Buffer Power Applications

Barber (1984) calculated  $D_e$  values for potassium and phosphorus using Eq. [10]. These soils were fertilized; hence

Figure 4-1. The difference in two buffer power definitions, as expressed by the ratio  $b'/b$ , at four water contents for a range of  $K_d$  values. When the ratio is 1,  $b$  approximates  $b'$ . The smaller graph (inset) enlarges the region where the ratio's converge to one.

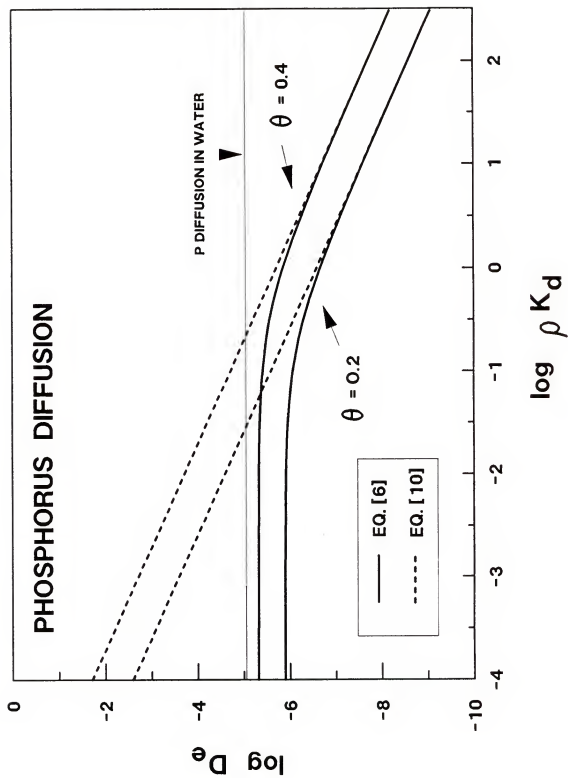


the assumption (i.e.,  $\rho K_d \gg \theta$ ) is probably valid that the amount of diffusible ions on the solid phase is greater than that in solution. For infertile forest soils of the southeastern coastal plain, however, this assumption does not hold true for phosphorus (i.e.,  $\rho K_d \leq \theta$ ). Surface soil of a Pomona fine sand was found to have  $\rho K_d$  and  $\theta$  values of 0.29 and 0.2, respectively. Furthermore, Humphreys and Pritchett (1971) and Ballard and Fiskell (1974) have also shown that values of  $K_d$  for phosphorus on many Lower Coastal Plain Spodosols are essentially zero. Thus, Eq. [10] would be incorrect for calculating  $D_e$ .

The effect of low  $\rho K_d$  values from these infertile soils on phosphorus  $D_e$  were compared using Eqs. [6] and [10]. For  $\rho K_d$  values greater than 15 times  $\theta$ , ( $\log \rho K_d = 0.5$  and  $0.8$  for  $\theta$  of  $0.2$  and  $0.4$ , respectively),  $D_e$  estimates by both equations were comparable (Fig. 4-2). However, for values of  $\rho K_d < 15\theta$ ,  $D_e$  estimates from Eq. [10] were approaching or greater than  $D_i$ , the diffusion of phosphorus in bulk water. Therefore Eq. [6] would be essential in order to determine reliable P diffusion coefficients for these infertile soils. Potassium  $D_e$  for these soils using Eqs. [6] and [10] is discussed in Appendix C.

Another situation where inherent assumptions may be violated is for the nitrate anion ( $\text{NO}_3^-$ ). Nitrate can be adsorbed (i.e.,  $K_d > 0$ ) by some Oxisols and Ultisols or excluded (i.e.,  $K_d < 0$ ), as occurs in some volcanic soils (van Genuchten

Figure 4-2. Comparison of phosphorus  $D_e$  using Eqs. [6] and [10] at two water contents for a range of  $K_d$  values. Phosphorus diffusion coefficient in water,  $D_l$  is  $8.9 \times 10^{-6} \text{ cm}^2 \text{ s}^{-1}$  and impedance,  $f$ , is  $3.9 \times 10^9$ .

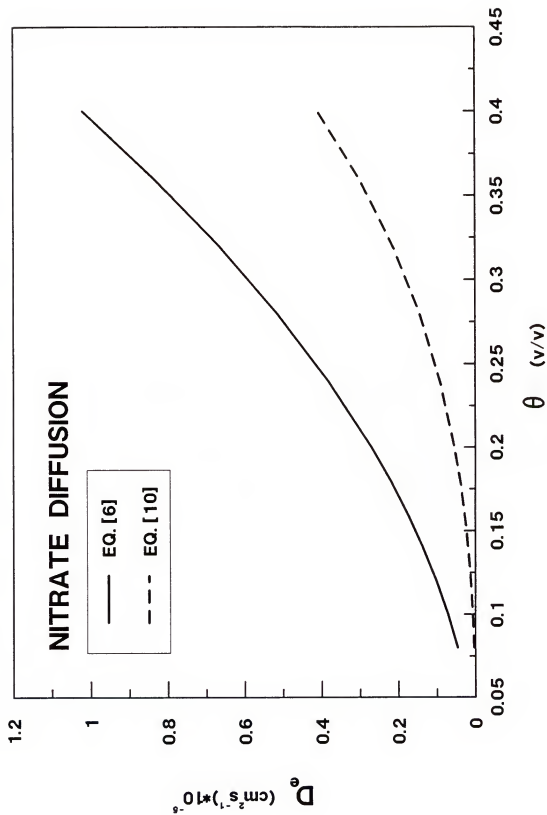


and Wierenga, 1986). However, for most soils,  $K_d$  is zero for nitrate (Kemper, 1986). Since Eq. [10] does not accommodate  $K_d$  values of 0,  $D_e$  would be undefined, making Eq. [10] conceptually incorrect. Therefore, the amount of nitrate in solution is important (i.e.,  $\rho K_d \neq 0$ ), and Eq. [6] must be used to determine reliable estimates of  $D_e$ .

In using Eq. [10], nitrate buffer powers have been reported to be 1, which assumed that nitrate was not absorbed to any appreciable extent (Barber and Cushman, 1981; Barber, 1984; Barber and Silberbush, 1984). However,  $b=1$  implies the opposite. If nitrate adsorption were assumed to be zero by using  $b=1$  in Eq. [10], then  $D_e$  could be greatly underestimated from the true case where  $K_d=0$  ( $b'=0$ ) in Eq. [6] (Fig. 4-3). For nonadsorbed ions ( $K_d=0$ ), the retardation factor (R) in Eq. [8], not  $b$  in Eq. [11], would be 1.

Although this discussion has centered around diffusion, the arguments favoring the use of Eq. [7] for buffer power are also valid in the context of nutrient replenishment to soil solutions. The application of Eq. [7] is essential in mechanistic nutrient uptake models, since both buffer power and diffusion estimates are integral processes in plant nutrient uptake predictions.

Figure 4-3. Comparison of nitrate diffusion at different water contents using Eq. [6] ( $K_d=0$  and  $b'=1$ ) and Eq. [10] ( $K_d=1$ ). Nitrate diffusion coefficient in water is  $1.95 \times 10^{-5} \text{ cm}^2 \text{ s}^{-1}$ , and impedance,  $f$ , is  $3.9 \times 10^4$ .



### Conclusions

Various definitions have been applied to nutrient "buffer power" of soils. Buffer power, as defined by Eq. [11], is valid only when the amount of diffusible ion on the solid phase ( $\rho K_d$ ) is substantially greater than that in the soil solution. Incorrect application of Eq. [11] can result in erroneous estimates of solute diffusion and of nutrient replenishment of soil solutions: parameters often used in nutrient uptake models. Since Eq. [7] is conceptually correct under any condition, we propose that the buffer power be defined as  $(\theta + \rho K_d)$  for future calculations of  $D_e$  and nutrient replenishment of soil solutions, in order to minimize the confusion already present in the literature.

CHAPTER 5  
MODELING POTASSIUM UPTAKE BY SLASH PINE SEEDLINGS  
FROM SOILS OF LOW POTASSIUM-SUPPLYING POTENTIAL  
OF THE SOUTHEASTERN COASTAL PLAIN

Introduction

Nutrient uptake, and hence plant growth, is influenced by conditions occurring at the soil-root interface. Although these conditions vary from site to site and from species to species, the processes and associated theory governing nutrient uptake should be applicable to all soils and plant species. The processes can be categorized into two broad groups: 1) the supply of nutrients in the soil, and 2) the absorption of nutrients at the root surface (Barber, 1979).

Nutrient supply in the soil is determined not only by nutrient levels in the soil solution, but by the soil's ability to replenish ions lost from the soil solution, and by the transport of these ions to the root via diffusion and mass flow. Nutrient absorption by the plant is affected by the extent of root surface area, root growth rate and nutrient influx at the root.

Integration of these processes to predict nutrient uptake has been accomplished only recently through the use of mathematical models. Comprehensive reviews of nutrient uptake processes are given by Olsen and Kemper (1968), Barley (1970),

Helyar and Munns (1975), Nye and Tinker (1977) and Barber (1984). Initial approaches to predicting nutrient uptake were based on theoretical consideration of the processes involved in ion flux to a single root growing in soil, ignoring root competition (Bouldin, 1961; Passioura, 1963; Nye and Spiers, 1964; Nye, 1966; Nye and Marriott, 1969).

Description of a single root, however, did not adequately reflect absorption by actively growing plant roots in soil. Therefore, root growth was incorporated into the simulation procedure (Brewster et al., 1976; Claassen and Barber, 1976). These simulations were the first to be validated using comparisons of predicted and observed uptake. Results, however, were variable.

Modifications intended to improve uptake predictions have included root competition (Cushman, 1979a,b; 1980; Claassen et al., 1986), root hairs (Itoh and Barber, 1983), root exudates (Nye, 1984a) and rhizosphere acidification (Nye, 1981, 1984b; Gillespie, 1988).

The Barber-Cushman model (Barber and Cushman, 1981) has been validated for phosphorus (P) and potassium (K) uptake by soybeans (Silberbush and Barber, 1983, 1984), for P and K uptake by corn (Schenk and Barber, 1980), for magnesium uptake by ryegrass (Rengel, 1988), and for cadmium and zinc uptake by corn (Mullins et al., 1986). One of the criticisms of nutrient uptake models based on diffusion/mass-flow supply theory, however, is that they have not been validated for

species growing in conditions other than fertilizer-amended soils (Clarkson, 1985). Clarkson suggested that the predictive powers of the models were considerably reduced at low concentrations, thus resulting in "ill-defined" factors which became important with respect to the efficiency of absorption.

The purpose, therefore, of this study was to (i) apply existing theories for nutrient uptake (via the Barber-Cushman and Baldwin-Nye-Tinker models) to determine potassium uptake by slash pine (*Pinus elliottii* Engelm. var. *elliottii*) seedlings grown in soils of low K-supplying potential under greenhouse and field conditions, (ii) determine the relative importance of each identified soil and plant parameter on K uptake by slash pine through model sensitivity analysis, and (iii) examine the uncertainty in predicted uptake estimates using a modified Monte Carlo simulation approach.

### Materials and Methods

#### Observed Potassium Uptake

Observed values for K uptake by slash pine seedlings were used to validate model predictions under three conditions: in a greenhouse environment; at a field site in the "Gator National Forest" (GNF), 10 km NE of Gainesville, FL; and at the Container Corporation of America tree nursery near Archer, FL.

Greenhouse study

Seedlings were grown in the greenhouse in soil material collected from the A horizon of a 4-year old (Pomona 1) and a 25-year old (Pomona 2) slash pine plantation at the GNF. The soils from both sites are classified as Pomona fine sand (sandy, siliceous, hyperthermic Ultic Haplaquods). The soils were air-dried, passed through a 2 mm sieve, and 1.5 kg of material was packed into each 3.5 L plastic pot using 12 pots per soil. Pots were flushed with 10 pore volumes of double-deionized water and then maintained at a water content of 0.18 and 0.12 (v/v) for Pomona 1 and Pomona 2, respectively, via daily additions of double-deionized water. Two additional pots of each soil, without seedlings, were used to measure daily water loss by evaporation.

Slash pine seeds (seed source 4; CCA 189-57, high-rust resistant and low-growth clones) were soaked overnight in water, and six seeds planted per pot. Pots were thinned to three seedlings 13 days after planting. Seedlings in each soil were harvested from two pots at 38 and 41 days, and from four pots at 55 and 81 days.

"Gator National Forest" study

Seedlings were grown in a 12\*1.2 m bed, divided into four compartments. The soil at this site was the same as the Pomona 1 soil of the greenhouse study. One month prior to planting, a 2% solution of glyphosate was applied to the bed to remove unwanted vegetation. Soil water potentials were

monitored with mercury manometer tensiometers installed in each compartment at depths of 10, 28 and 45 cm, corresponding to the centers of the A, E, and Bh horizons, respectively. The site was watered daily with well water. Water potentials were measured before and after watering and water contents were determined from potentials using the procedure of van Genuchten (1978) (Appendix D).

Slash pine seeds (seed source 4) were soaked overnight and then planted in flats in the greenhouse. Thirteen days after sowing, 80 seedlings were transplanted to each compartment in the field (Time 1). Six seedlings were harvested from each compartment at 13, 18, 32, 53 and 81 days after sowing in the greenhouse.

A second replication in time (Time 2), of the study described above, was initiated two weeks after the start of the first experiment (Time 1). An additional forty seedlings were transplanted into each compartment. Six seedlings from this planting were harvested from each compartment at 13, 53 and 81 days after sowing. All seedlings were harvested by carefully excavating roots of each tree in the A horizon, and recording lengths of the taproot and the longest lateral.

#### Nursery study

Soil at the tree nursery site was classified as Millhopper sand (loamy, siliceous, hyperthermic Grossarenic Paleudults). The section of bed (30\*1.2 m) selected for the study was subjected to standard management procedures for the

nursery. The beds were first fumigated and then sown (8 rows per bed) with slash pine seeds (seed source 3; high-growth and high rust-resistant clones), to produce 330 seedlings  $\text{m}^{-2}$ . Fertilization consisted of 392 kg  $\text{ha}^{-1}$  of SUL-PO-MAG (22%  $\text{K}_2\text{O}$ , 18%  $\text{MgO}$ , and 22% sulphur) one month prior to planting followed by two applications of 224 kg  $\text{ha}^{-1}$  of 10-10-10 material at 40 and 48 days after planting.

Soil moisture potentials were measured daily, using vacuum-gauge tensiometers installed at a depth of 15 cm. Water contents were calculated as described above.

Four replicates of 10 seedlings each were harvested at 8, 15, 22, 29, 36, 43 and 50 days after sowing seed on 1 May 1987. Seedlings were harvested by removing a cylindrical column (8 cm in radius and 30 cm deep) of soil around each replicate of seedlings.

#### Laboratory Analysis

At each harvest, seedling roots were rinsed briefly with deionized water, weighed, and root lengths measured by the line-intercept procedure (Newman, 1966). Roots and shoots were then dried at 60°C, weighed, dry-ashed and analyzed for K by atomic absorption spectroscopy using 2% cesium (Cs), added to suppress ionization. Thinned seedlings from the greenhouse study were also analyzed by the above procedure to determine initial root lengths and K contents.

Soils of this study covered a range of soil physical and chemical properties, as shown in Table 5-1. All soil samples

Table 5-1. Chemical and physical data for the soils used in the greenhouse (Pomona 1 and 2) and field (GNF and Nursery) experiments.

Expt.	Bulk Density	pH	O.M.	CEC	Mehlich-I K	NH <sub>4</sub> OAc K
	Mg m <sup>-3</sup>		%	cmol kg <sup>-1</sup>	----- μg g <sup>-1</sup> -----	
Pomona 1	1.42	4.02	4.62	2.57±0.40 <sup>a</sup>	12.8±0.5	16.9±0.3
Pomona 2	1.47	4.03	1.94	1.43±0.05	6.7±0.5	8.6±0.4
GNF	1.38	4.02	3.63	2.05±0.09	5.2±1.8	6.3±0.8
Nursery	1.58	4.64	1.65	1.24±0.06	19.4±4.0	23.5±0.4

a Mean and SE.

were analyzed for bulk density, pH, CEC, OM, exchangeable K and extractable K. The pH was measured in deionized water using a 1:2 soil to solution ratio. Organic matter was determined by the Walkley-Black procedure (Nelson and Sommers, 1982). Exchangeable K was determined by extracting the soil with  $\text{NH}_4\text{OAc}$  (Knudsen et al., 1982), while extractable K was measured using the Mehlich-I procedure ( $0.025 \text{ M H}_2\text{SO}_4 + 0.05 \text{ M HCl}$ ) with a 1:10 soil-extractant ratio. Cation exchange capacity was determined by the barium chloride method described by Hendershot and Duquette (1986).

#### Predictions of Potassium Uptake

##### Barber-Cushman model (BCM)

The Barber-Cushman nutrient uptake model uses 11 soil and plant parameters to calculate nutrient flux to the root and subsequent ion absorption at the root surface. A list of the major assumptions are presented in Appendix E. A more detailed discussion of the mathematical equations and assumptions used in the model can be found in Barber and Cushman (1981) and Barber (1984). The computer program was supplied by Dr. S.A. Barber of Purdue Univ. and all simulations were performed on an IBM compatible microcomputer (Oates and Barber, 1987).

##### Estimation of soil parameters

Four parameters are used to describe nutrient flux to the root in both models: the initial concentration of K in the soil solution ( $C_{11}$ ); the soil's ability to replenish K lost

from soil solution, known as the buffer power ( $b'$ ); the effective diffusion coefficient ( $D_e$ ) of K in soil; and the average water influx ( $V_0$ ). Units of measurement for all soil and plant parameters are found in the accompanying tables.

Initial K concentrations were determined using soil samples collected at the beginning of each study. Soil solution samples were extracted by centrifugation, similar to the procedure of Elkhatib et al. (1987). Soil solution samplers were used for the nursery.

The buffer power ( $b'$ ) is defined (see Chapter 4) as:

$$b' = \theta + \rho K_d \quad [1]$$

where  $\theta$  is the volumetric water content;  $\rho$  is the bulk density of the soil; and  $K_d$  is described by  $\partial C_s / \partial C_l$ , where  $C_s$  is the concentration of K ( $\mu\text{mol g}^{-1}$ ) on the solid phase which equilibrates with  $C_l$ , the K concentration ( $\mu\text{mol cm}^{-3}$ ) in solution. Average values of  $K_d$  were determined from the slopes ( $C_s/C_l$ ) of desorption isotherms, using a dilution method. Varying amounts of soil were combined with 40 ml of 0.16 mM solution (electrical conductivity (EC) at  $22^\circ\text{C} = 46 \mu\text{mhos cm}^{-1}$ ) of  $\text{CaCl}_2$ , adjusted to a pH of 4.5, to yield soil-solution ratios of 1:5, 1:10, 1:20, and 1:40. Each soil was replicated at each dilution. Solutions were placed on a rotary shaker for 24 hours and then filtered through Whatman #1 filter paper. The filtrate was then analyzed for EC and K concentration by atomic absorption spectroscopy using 2% Cs to suppress ionization. Electrical conductivities were used

to estimate activity coefficients (Lindsay, 1979), in order to calculate K activities. Differences between K activities and K concentrations were < 3%, making these respective values essentially the same. The K released into solution ( $\mu\text{mol g}^{-1}$ ) and the K activities ( $\mu\text{M}$ ) were used to plot desorption isotherms. Potassium desorption was assumed to be instantaneous, reversible, and linear over the range of  $C_s$  and  $C_l$ .

Fertilizer additions to the soil at the nursery site were incorporated into a separate K uptake simulation. To predict K uptake, the amount of K in the fertilizer amendment was partitioned between the solid phase ( $C_s$ ) and the soil solution phase ( $C_{li}$ ) using the soil's buffer power. The inherent assumptions are that this partitioning occurred uniformly throughout the rooting zone, that adsorption of K onto the solid phase was instantaneous, that  $b'$  and  $D_e$  were not affected by increasing  $C_{li}$ , and that there was no leaching of K in the soil profile.

Values for  $D_e$  were calculated from the equation of Nye (1968) and of Olsen and Kemper (1968):

$$D_e = D_L \theta f / (\theta + \rho K_d) \quad [2]$$

where

$$f = 3.1 \theta^{1.9}. \quad [3]$$

The diffusion coefficient for K in water ( $D_L$ ) is  $1.98 \times 10^{-5} \text{ cm s}^{-1}$ , and  $f$  is the impedance factor which accounts for the tortuous pathway of ions through soil pore sequences. The

impedance factor was determined by a non-linear least squares procedure (SAS Institute Inc., 1982), using impedance/water content data from Porter et al. (1960), Rowell et al. (1967), Warncke and Barber (1972) and Barraclough and Tinker (1981) (Appendix C; Fig. C-1).

Water influx rate in the greenhouse study was calculated from the total amount of water lost from a given pot minus the water lost by evaporation. Average water influx ( $V_o$ ) was calculated from the equation of Williams (1946):

$$V_o = U / [(T_2 - T_1)(L_2 - L_1) 2\pi r_o] \quad [4]$$

where  $U$  is the total amount of water transpired during the growth period  $T_2 - T_1$ ,  $L_2$  is the root length at time  $T_2$ , and  $L_1$  is the root length at time  $T_1$ . The  $V_o$  estimates from the greenhouse study were also used for seedlings grown at the GNF and nursery sites.

#### Estimation of plant parameters

The seven plant parameters required to simulate nutrient uptake include those characterizing root amount and morphology, and those which relate to ion influx kinetics.

The plant root system was described by the root radius ( $r_o$ ), mean half-distance between roots ( $r_1$ ), and root growth rate ( $k$ ). The rate of root growth was assumed to be linear with time for all studies, with  $k$  being calculated as:

$$k = (L - L_o) / (T - T_o) \quad [5]$$

where  $L_o$  is the initial root length at time ( $T_o$ ) and  $L$  is the root length at harvest time  $T$ . Average root radius was

calculated from the equation:

$$r_o = [F_{wr}/(\pi L)]^{1/2} \quad [6]$$

where  $F_{wr}$  is the fresh root weight and  $L$  is the total root length. This equation assumes a root density of  $1 \text{ Mg m}^{-3}$ . The half-distance between roots was calculated as:

$$r_i = 1/(\pi L_v)^{1/2} \quad [7]$$

where  $L_v$  is the rooting density.

Potassium net influx ( $I_n$ ) at the root surface was assumed to follow Michaelis-Menten kinetics (Claassen and Barber, 1974):

$$I_n = I_{\max}(C_r - C_{\min})/[K_m + (C_r - C_{\min})] \quad [8]$$

where  $I_{\max}$  is the maximum ion influx rate;  $K_m$  is the Michaelis-Menten constant and is defined as the the ion concentration at  $\frac{1}{2} I_{\max}$ ;  $C_r$  is the ion concentration at the root surface; and  $C_{\min}$  is the ion concentration when net influx is 0. These parameters were calculated from data for year-old slash pine seedlings grown in nutrient solutions (Chapter 2). Average values from these studies resulted in an  $I_{\max}$  of  $3.61 \times 10^{-6} \text{ } \mu\text{mol cm}^{-2} \text{ s}^{-1}$ , a  $K_m$  of  $.0287 \text{ } \mu\text{mol cm}^{-1}$ , and a  $C_{\min}$  of  $.001 \text{ } \mu\text{mol cm}^{-1}$ .

Student t-tests were used to determine if slopes between observed and predicted nutrient uptake values were significantly different from one at a P level of 0.05.

#### Baldwin-Nye-Tinker model (BNTM)

A steady-state approach was developed by Nye and Spiers (1964), Nye and Marriott (1969) and Baldwin et al. (1973). This model differs from the BCM in two major assumptions: 1)

the BNTM assumes steady-state soil water and solute conditions, which results in a steady-state depletion profile near the root, whereas the BCM only assumes steady-state soil water conditions; and 2) the BNTM assumes that nutrient flux at the root surface is linearly related to nutrient concentration at the root surface (i.e.,  $K_m \gg C_r$  and  $I_n = (I_{max}/K_m)C_r$ ), while the BCM employs a nonlinear boundary condition at the root surface (i.e., Eq. [7]). These simplifying assumptions (along with the others listed in Appendix E) for the steady-state approach facilitate a simple approximate solution for predicting K uptake, while a numerical approach must be used for the Barber-Cushman model. For a more detailed discussion of the assumptions and equations of the steady-state approach, the reader is referred to Nye and Marriott (1969), Baldwin et al. (1973) and Nye and Tinker (1977).

Parameters which are similar to those of the Barber-Cushman model for predicting K uptake include  $C_{11}$ ,  $b'$ ,  $D_e$ ,  $V_o$ , and  $r_o$ . Nutrient influx, however, is described by a constant  $\alpha$  ( $I_{max}/K_m$ ), the root absorption coefficient (Nye, 1966; Nye and Tinker, 1969); and initial root length and root growth rates are expressed per unit volume of soil as  $L_v$  and  $k_v$ , respectively.

Simulations for the steady-state approach were run for all studies, including fertilizer additions at the nursery site. Predicted K uptake from the simple approximate solution

of the BNTM were then compared to the more exact numerical solutions of the BCM simulations to determine the usefulness of the BNTM under actual soil conditions.

#### Sensitivity Analysis

Sensitivity analysis was conducted with the BCM to evaluate the effect of each parameter on K uptake, when considering all parameters to be independent of one another. Simulations of K uptake were conducted by varying each parameter between 0.25 and 2.0 times its measured value. While each parameter was changed, the remaining parameters were held constant at their initial values. Results are expressed relative to predicted K uptake under the initial conditions.

#### Monte Carlo Simulations

Modified Monte Carlo simulations for K uptake were calculated using estimates from the population distributions of each parameter in the BCM. Simulations were run for seedlings harvested after approximately 21 and 42 days for the nursery and GNF studies, respectively. Population distributions were calculated for each parameter using the parameter mean ( $\mu$ ) and SD ( $\sigma$ ) along with a set of 1000 uniform, random numbers. Random numbers (R) were generated by a congruent multiplicative technique and normalized using the Box and Muller procedure (Kennedy and Gentle, 1980). Normal and log-normal distributed parameters were calculated separately.

### Parameters with normal distributions

Normally-distributed parameters for uptake include  $\rho K_d$ ,  $C_{li}$ ,  $r_1$ ,  $r_o$ ,  $k$ ,  $L_o$ ,  $K_m$  and  $C_{min}$ . However,  $r_1$ ,  $L_o$  and  $k$  are a function of the measured root length. Therefore, population distributions for these parameters were calculated using an estimate of the root length population distribution. The standard deviation associated with the total root length was assumed to be 10% of its measured value. This standard deviation was also used for  $L_o$ .

Population distributions for these parameters were calculated from the equation:

$$N = R\sigma + \mu \quad [9]$$

where  $N$  is an estimate of the distribution.

### Parameters with log-normal distributions

Water flux and  $I_{max}$  were assumed to have log-normal distributions, since they are classified as intensity factors. The diffusion coefficient was calculated from an estimate of  $\theta$ , which was based in turn on a log-normal distribution of the water potential. The impedance factor was then calculated from these soil water contents, and used along with the  $\rho K_d$  values from above to calculate  $D_e$ .

Log-normal distributions were based on the equation

$$N = \exp(R\beta + \alpha) \quad [10]$$

where  $\alpha$  and  $\beta$  are the log-normal mean and standard deviation, respectively. They are calculated using the following two

equations of Yevjevich (1972):

$$\alpha = \frac{1}{2} \ln[\mu^4/(\mu^2 + \sigma^2)] \quad [11]$$

$$\beta^2 = \ln[(\sigma^2 + \mu^2)/\mu^2] \quad [12]$$

where  $\sigma$  and  $\mu$  have the same definitions as before.

Simulations were terminated when the total variance for K uptake remained constant (nursery,  $n = 400$  simulations; GNF,  $n = 200$  simulations). Frequency distributions of the simulations were tested for normality by the Shapiro-Wilk statistic (SAS Institute Inc., 1985).

## Results

### Predicting K Uptake using the Barber-Cushman Model

The ranges in soil and plant parameters for each study as used to predict K uptake are listed in Table 5-2. A complete list of parameter estimates for each simulation can be found in Appendix A.

### Greenhouse study

Over the duration of the greenhouse study, BCM predicted K uptake was 1.31 and 1.50 (both significantly different from 1) times greater than K levels observed for seedlings grown in the Pomona 1 and Pomona 2 soils, respectively (Fig. 5-1). There was a strong correlation, however, between predicted and observed results. Potassium uptake showed good agreement between predicted and observed uptake for earlier seedling harvests: Pomona 1, slope = 0.81,  $r^2 = 0.79$  at 25 days; and Pomona 2, slope = 1.12,  $r^2 = 0.91$ , at 42 days. These slopes

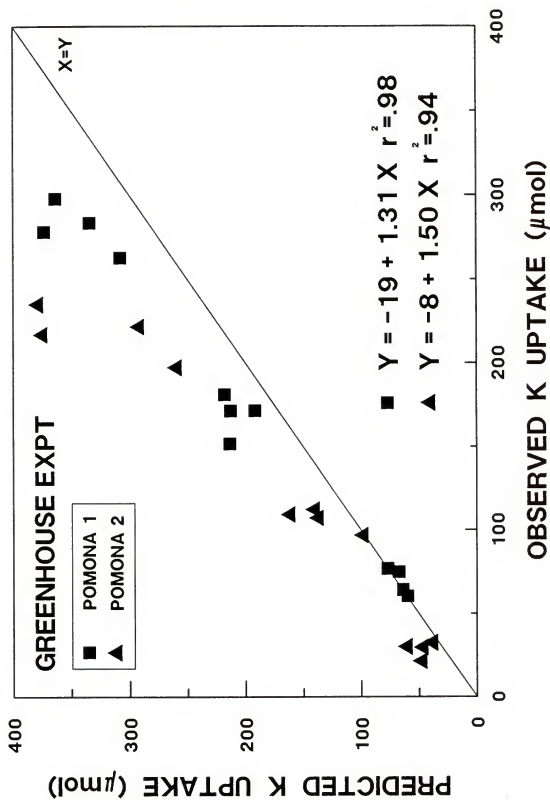
Table 5-2. Range in soil and plant input parameters for each study.

Parameter	Greenhouse		Gator National Forest		Nursery
	Pomona 1	Pomona 2	Time 1	Time 2	
$D_e$ (cm <sup>2</sup> s <sup>-1</sup> )*10 <sup>-7</sup>	0.99-1.04	0.20-0.26	Soil Parameters		
			2.91-6.28	3.43-4.46	0.21-0.68
$b'$	3.64	6.11	3.00-3.44	3.00-3.44	6.26
$C_{li}$ (μmol cm <sup>-3</sup> )	0.136	0.093	0.035-0.06	0.035-0.06	0.203
$V_o$ (cm s <sup>-1</sup> )*10 <sup>-6</sup>	2.23-4.07	2.26-10.35	3.79	3.79	3.79
			Plant Parameters		
$r_1$ (cm)	0.84-1.54	0.62-2.02	1.7-3.15	1.39-2.87	0.75-2.59
$r_o$ (cm)	0.038-0.042	0.036-0.043	0.038-0.060	0.036-0.044	0.027-0.046
$L_o$ (cm)	11.9	11.9	16.6-28.9	25.1-31.6	41.3
$L_v^a$ (cm cm <sup>-3</sup> )	0.0059	0.0059	0.0019-0.06	0.0014-0.23	0.006-0.023
$k$ (cm s <sup>-1</sup> )*10 <sup>-4</sup>	1.16-1.97	0.64-2.64	0.12-1.51	0.28-1.84	0.86-4.55
$k_v^a$ (cm cm <sup>-3</sup> s <sup>-1</sup> )*10 <sup>-8</sup>	5.57-9.12	3.29-13.62	0.49-10.0	0.66-4.03	4.72-9.08
$I_{max}$ (μmol cm <sup>-2</sup> s <sup>-1</sup> )*10 <sup>-6</sup>	3.61	3.61	3.61	3.61	3.61

Table 5-2. Continued

Parameter	Greenhouse		Gator National Forest		Nursery
	Pomona 1	Pomona 2	Time 1	Time 2	
----- Plant Parameters -----					
$K_m$ ( $\mu\text{mol cm}^{-3}$ )	0.029	0.029	0.029	0.029	0.029
$\alpha^a$ ( $\text{cm s}^{-1}$ ) $\ast 10^{-4}$	1.26	1.26	1.26	1.26	1.26
$C_{\text{min}}$ ( $\mu\text{mol cm}^{-3}$ )	0.001	0.001	0.001	0.001	0.001
t (days)	38-81	38-81	11-81	11-81	8-50
$\theta$ ( $\text{cm}^3\text{cm}^{-3}$ )	0.17	0.12	0.24-0.30	0.25-0.27	0.12-0.17
for BNTM					

Figure 5-1. Comparison of predicted K uptake by the Barber-Cushman model and observed K uptake for pot-grown slash pine seedlings in the greenhouse.



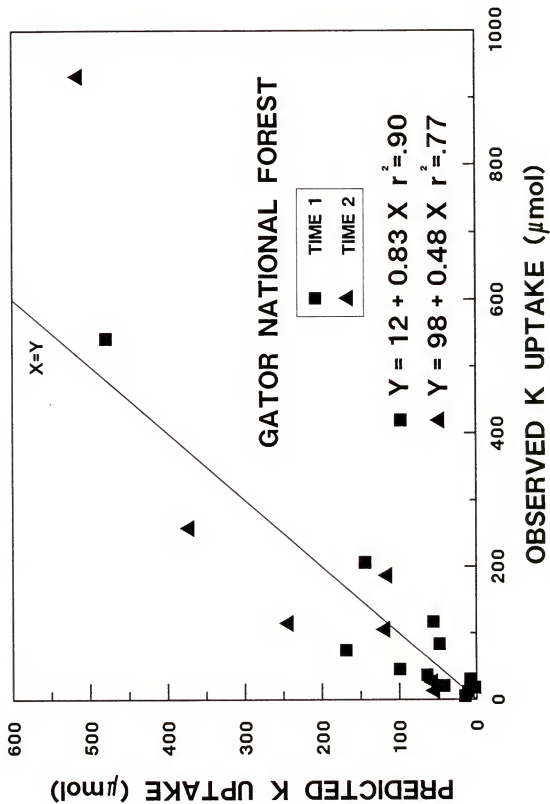
were not significantly different from 1. At later harvests, however, the simulations tended to overestimate K uptake. Observations during the last two seedling harvests indicated that roots were growing on the pot bottom and along pot walls. External fungal hyphae associated with mycorrhizal infection of the root were not seen.

"Gator National Forest" study

Potassium uptake was significantly underpredicted in this case, with uptake being 0.83 and 0.48 that of the observed K values for Times 1 and 2, respectively (Fig. 5-2). The underprediction was more evident for Time 2, where the data were more variable. Elimination of one harvest value (observed K = 875  $\mu\text{mol}$ ), however, would result in a slope of 1.08 (not significantly different from 1), but a  $r^2$  of only 0.66. After the second harvest (21 days), external mycorrhizal fungal hyphae were evident and abundant.

A conservative estimate for fungal-hyphae uptake by seedlings at the GNF was made using the uptake model. Assumptions for this simulation included the same influx parameters, interroot distances, and soil parameters as used for pine root uptake (Table 5-2; using GNF, Time 1); total hyphae length an order of magnitude greater than pine root length; and an average hyphae radii of 1.5  $\mu\text{m}$  (Bowen, 1973). Simulations showed that K uptake was increased from 0.83 to 0.94 ( $r^2 = 0.89$ ) times the observed value, an 11% increase over the estimates for pine roots alone.

Figure 5-2. Comparison of predicted (BCM) and observed K uptake for seedlings grown in the field at the Gator National Forest. Time 1 and Time 2 represent experiment replications at different times.



### Nursery study

Potassium uptake (uncorrected for fertilization) over a seven-week period was underpredicted by a factor of 0.70 for the nursery site (Fig. 5-3). Even though the underprediction was significantly different from one, there was a strong correlation between predicted and observed values. Like the greenhouse study, predicted uptake for early harvests was similar to observed values (slope =0.89,  $r^2$  =0.81; not significantly different from 1). With time, however, simulated K uptake tended to underestimate the amount of K in the seedlings.

Deviations of predicted K uptake from the 1:1 relationship, however, occurred after the application of fertilizer. When the simulations were rerun, accounting for the increase in soil solution concentrations following fertilizer amendments, predicted K uptake over the seven week period was now only 7% higher (NS different from 1,  $P=0.01$ ) than K uptake observed for the seedlings (Fig. 5-3).

External mycorrhizal hyphae from seedlings were not seen during any harvest.

### K Uptake using the Steady-State Approach

For all studies, K uptake predicted by the steady-state approach (BNTM) was 5% higher (significantly different from 1,  $P=0.05$ ) than predicted by the Barber-Cushman simulations (Fig. 5-4). Small deviations from the 1:1 correlation

Figure 5-3. Comparison of predicted (BCM) and observed K uptake by slash pine seedlings at the tree nursery. Fertilization arrows represent applications of 224 kg ha<sup>-1</sup> of 10-10-10 material during the experiment. Regression of K uptake with fertilization, includes both the data points prior to fertilization (■) and those following fertilizer applications (\*).

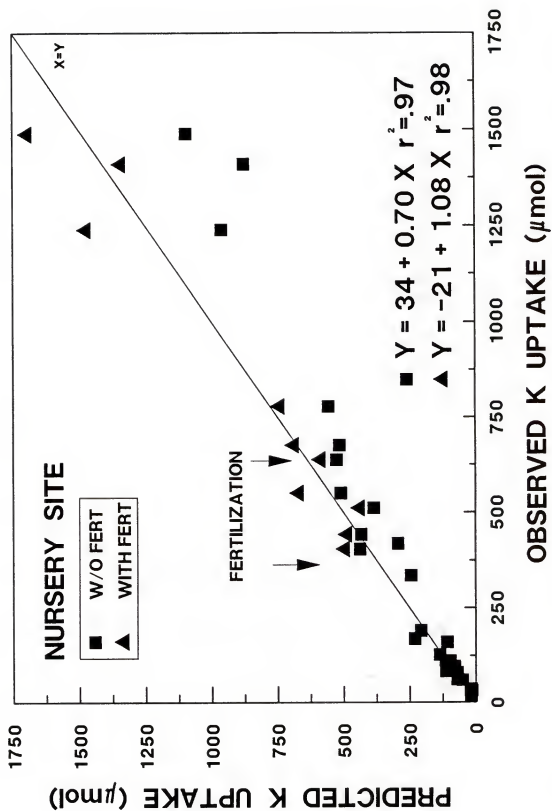
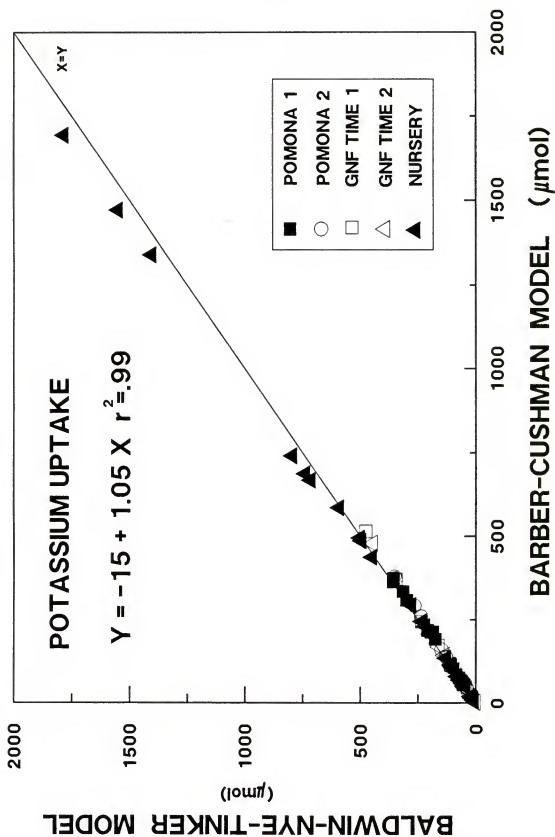


Figure 5-4. Comparison of predicted K uptake for slash pine seedlings by the Baldwin-Nye-Tinker model (BNTM) and the Barber-Cushman model (BCM). All seedling harvests are included.



occurred at the larger values of predicted uptake for the nursery site.

### Sensitivity Analysis

General trends of the sensitivity analysis for the Pomona 1 and Pomona 2 soils were similar to those of the GNF and nursery studies, respectively; therefore, only the soil and plant factors from Pomona 1 (Figs. 5-5a,b) and Pomona 2 (Figs. 5-6a,b) will be presented.

For all three studies, the initial soil solution concentration ( $C_{ii}$ ) and the root growth rate ( $k$ ) were the two most sensitive factors influencing uptake. When these parameters were changed by a factor of two, uptake increased linearly by as much as 90 to 99%. Sensitivity of the other parameters with respect to K uptake in the Pomona 1 study, in order of decreasing importance, were  $r_o > V_o \gg b' > D_e$ . This order was altered for the Pomona 2 study, where  $b' \gg r_o, D_e \gg V_o$ . The half-distance between roots became significant with respect to K uptake only when  $r_1$  was decreased below a relative change of 0.5. Changing the Michaelis-Menten kinetic parameters  $I_{max}$ ,  $K_m$  and  $C_{min}$  had little effect either on increasing (<3%) or decreasing (<6%) K uptake.

### Monte Carlo Simulations

Frequency distributions of K uptake for the modified Monte Carlo simulations were based on the means and SDs of parameters in Table 5-3. Distributions of K uptake were normally distributed ( $P=0.0015$ ) for the GNF site, with a

Figure 5-5. Sensitivity analysis of K uptake for slash pine seedlings grown in the Pomona 1 soil. Results are expressed relative to K uptake under the initial conditions, with each parameter being changed independently of the others. Top graph (a) represents the soil parameters ( $D_e$  - diffusion coefficient;  $b'$  - buffer power;  $C_{li}$  - initial K solution concentration and  $V_o$  - water flux) while the bottom graph (b) contains the plant parameters affecting uptake ( $k$  - root growth rate;  $r_o$  - root radius;  $r_1$  - mean interroot distance;  $I_{max}$ ,  $K_m$  and  $C_{min}$  are Michaelis-Menten parameters).

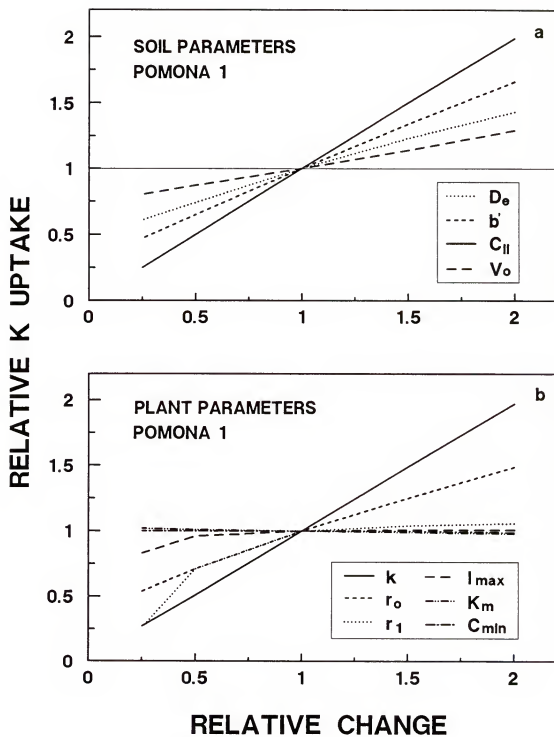


Figure 5-6. Sensitivity analysis of K uptake for slash pine seedlings grown in the Pomona 2 soil. Results are expressed relative to K uptake under the initial conditions, with each parameter being changed independently of the others. Top graph (a) represents the soil parameters ( $D_e$  - diffusion coefficient;  $b'$  - buffer power;  $C_{1i}$  - initial K solution concentration and  $V_o$  - water flux) while the bottom graph (b) contains the plant parameters affecting uptake ( $k$  - root growth rate;  $r_o$  - root radius;  $r_i$  - mean interroot distance;  $I_{max}$ ,  $K_m$  and  $C_{min}$  are Michaelis-Menten parameters).

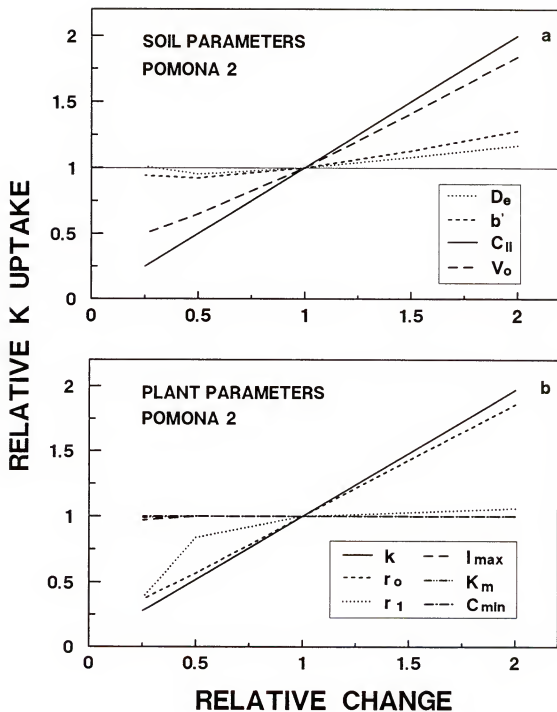


Table 5-3. Means and standard deviations of input parameters for the Monte Carlo simulations.

Parameter	GNF	Nursery
$D_e$ ( $\text{cm}^2 \text{ s}^{-1}$ ) $\times 10^{-7}$	4.83 $\pm$ 3.71	5.20 $\pm$ 4.17
$\rho K_d$	3.17 $\pm$ 0.82	6.09 $\pm$ 0.61
$C_{11}$ ( $\mu\text{mol cm}^{-3}$ )	0.048 $\pm$ 0.002	0.203 $\pm$ .083
$V_o$ ( $\text{cm s}^{-1}$ ) $\times 10^{-6}$	3.79 $\pm$ 2.12	3.79 $\pm$ 2.12
$r_1$ (cm)	2.01 $\pm$ 0.10	1.62 $\pm$ 0.08
$r_o$ (cm)	0.048 $\pm$ 0.006	0.031 $\pm$ 0.004
$L_o$ (cm)	19.4 $\pm$ 1.9	41.3 $\pm$ 4.1
$k$ ( $\text{cm s}^{-1}$ ) $\times 10^{-4}$	0.52 $\pm$ 0.06	2.37 $\pm$ 0.26
$V_{\max}$ ( $\mu\text{mol cm}^{-2} \text{ s}^{-1}$ )	(3.61 $\pm$ 2.56) $\times 10^{-6}$	
$K_m$ ( $\mu\text{mol cm}^{-3}$ )	0.029 $\pm$ 0.022	
$C_{\min}$ ( $\mu\text{mol cm}^{-3}$ )	0.001 $\pm$ .0005	
$t$ (sec)	3629100	1821000
$h$ (cm of water)	38 $\pm$ 17	100 $\pm$ 32

relatively small CV of 34% (Fig. 5-7a). Distributions for the forest tree nursery had a significant number of estimates that were at least 2 times the mean, resulting in a positive skewness and a much higher CV (57%) (Fig. 5-7b).

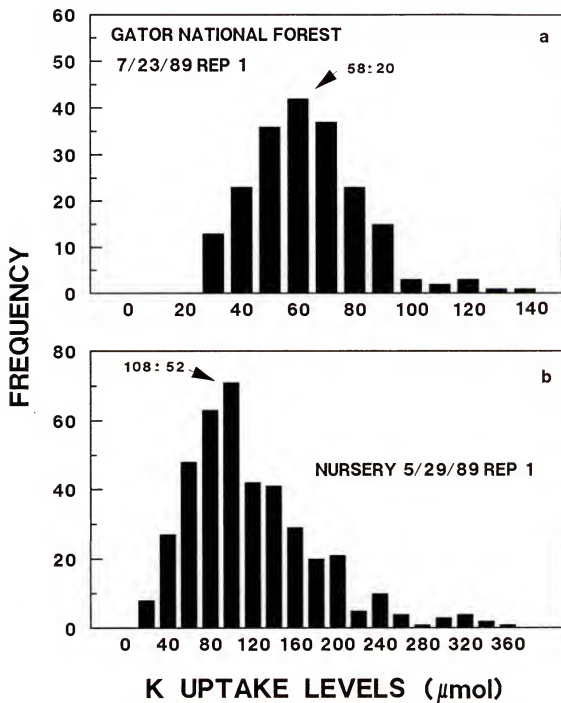
## Discussion

### Modeling K Uptake

Mechanistic nutrient uptake models have been applied almost exclusively, and with much success, to agronomic crops growing in fertilized soils (Schenk and Barber, 1980; Silberbush and Barber, 1983, 1984; Mullins et al., 1986; Rengel, 1988). Application of this approach to tree seedlings grown in soils of low K-supplying potential also resulted in reasonable predictions of K uptake. Therefore, the conceptual completeness and level of complexity of the processes developed in these models appears to be satisfactory for predicting nutrient uptake under a wide variety of conditions. The close similarity between the BCM and BNTM simulations shows that further simplifications which assume steady-state conditions and constant nutrient influx are in general valid, and should be useful for investigating nutrient uptake on soils of low nutrient-supplying potential.

The greenhouse simulations were strongly correlated with observed values, and mimicked K uptake quite well up to 41 days. After this point, however, overestimates of K uptake resulted. The early conformance between uptake and

Figure 5-7. Monte Carlo simulations of K uptake for one harvest: a) at the Gator National Forest, and b) at the tree nursery. Arrows represent mean and SD values.



predictions gives one confidence in the applicability of the theory. Deviations from the simulations, therefore, suggest that the overpredictions are due to a violation of model assumptions or to improperly defined input parameters.

A basic assumption of both models requires roots to be uniformly distributed and parallel (Baldwin and Tinker, 1972; Nye and Tinker, 1977). The BCM further requires that roots are constantly growing into new soil. Both assumptions were violated after the first harvest in the greenhouse study, when roots began growing along pot sides. The logical outcome of this condition is an overprediction of uptake.

Simulations for the GNF showed a reasonable agreement with observed values, with no significant trends away from the 1:1 correlation, except for the last harvest. By 81 days, however, underestimates were outside the limits of model prediction intervals, as defined by the Monte Carlo simulations. Several explanations, ranging from significant root growth below the sampling zone (the A horizon) to increased K uptake by mycorrhizal infected roots, are plausible. There was no observational evidence that roots had proliferated below the A horizon during the study. Mechanistic simulations assume, however, that roots are smooth cylinders and that nutrient influx is not affected by mycorrhizae or by root hairs (Barber, 1984). Rygielwicz and Bledsoe (1984) provided evidence that mycorrhizal roots had higher rates of K uptake than non-infected roots. Sensitivity

analysis, however, showed that K uptake predictions were insensitive to increases in  $I_{\max}$  and  $K_m$  values. Therefore, even though mycorrhizal roots were plentiful on seedling at later harvests, the higher influxes by these roots would have little effect on increasing K uptake in model simulations.

Although the simulation of K uptake by hyphae growing in the soil used a very conservative approach, it suggests the potential importance of hyphae strands in K uptake from these soils. The major limitation in simulating hyphae uptake is our inherent inability to measure the amount of symbiotic hyphae in the soil. Sensitivity analysis also indicates that the amount of root absorbing surface area (i.e., sensitivity to K concentration) is a major factor affecting uptake. Therefore, exclusion of fungal hyphae is the most plausible reason for the underpredictions in K uptake, especially for the last harvest at the GNF.

The simulations for the forest tree nursery are a good example of the practical application of this approach. The data show that fertilization can be effectively modeled. For managers who set target goals with respect to seedling nutrient contents at lifting, this technique can be used to plan both fertilizer schedules and amounts.

#### Sensitivity Analysis

Root growth rate ( $k$ ) and root radius ( $r_o$ ) were the only two plant parameters to which K uptake was sensitive. Each of these parameters represents the amount of root surface area

available for nutrient uptake; hence, for the soils of low K-supplying potential in this study, the amount of effective absorbing root appears to be crucial. The significance of these parameters in K uptake, therefore, underscores the importance of obtaining accurate and mechanistically-independent estimates of root length and growth.

One drawback to the approach taken in this study is that root length and growth are the only parameters which are not truly independent estimates, but are instead measurements based on the harvested seedlings. Thus, the challenge in future nutrient uptake simulations is to incorporate a mechanistically derived approach for determining root growth, while not adding such a high degree of uncertainty to the predicted estimates that they become meaningless.

The unimportance of the Michaelis-Menten parameters is a result of the inherently low K-supplying power of these soils. Therefore,  $C_r$  was sufficiently reduced to cause nutrient uptake to occur in the linear portion of the Michaelis-Menten curve, where  $I_n \ll I_{max}$ . This condition also may be a partial explanation for the good agreement between BCM and BNTM in our studies. With the lower values of  $C_r$ , the BNTM assumption of a linear form of the Michaelis-Menten relationship was never violated. For conditions of greater soil supply, however, one would expect the BNTM to overpredict uptake compared to the BCM as  $C_r$  increases. The  $C_{11}$  was the soil parameter to which K uptake was most sensitive. Unlike

the plant parameters, however, all soil parameters had some effect with respect to increased uptake. The relatively high degree of sensitivity of the soil parameters, coupled with the insensitivity of the Michaelis-Menten parameters, suggests that soil processes were the rate-limiting step to K acquisition by seedlings in our studies. This was confirmed by determining the ratio of the root absorbing power to the combined processes of diffusion and mass flow (i.e.,  $\alpha r_o / [D_L \theta f / \ln(r_1 / 1.65 r_o) + V_o r_o]$ ; Nye, 1977). Ratios ranged from 7.5 to 24, indicating that the rate of supply for K was much smaller than the rate at which K could be absorbed at the root surface.

The importance of each of the soil variables and their different rankings for soils that are quite similar in morphology emphasizes the complexity of soil nutrient supply to trees on these sites. Therefore, soil tests indexing only the amount of K on a given site may have limited value for separating sites of different K-supplying power, since such tests do not take into account the partitioning of ions between solution and solid phases, the differences in soil water regime, and the efficiency of the root surface for nutrient absorption.

### Conclusions

Prior mechanistic approaches to modeling nutrient uptake have been restricted primarily to agronomic situations. This

approach was also successfully validated for predictions of K uptake by slash pine seedlings grown on soils of low K-supplying potential. Therefore, the conceptual completeness and level of detail developed in the model appears to be satisfactory for predicting nutrient uptake under a wide variety of conditions.

Potassium uptake was overpredicted by 31 to 50% in greenhouse studies; overestimates, however, are attributed to non-uniform distribution of roots along pot walls. The model underpredicted K uptake by 0.48 to 0.83 times that observed in field-grown seedlings. Although external fungal hyphae were abundant in the field, their contribution to K uptake was not included, suggesting the potential importance of hyphae in uptake processes. Predictions of K uptake were excellent for seedlings grown at the tree nursery when fertilizer amendments were included. Simplifications of the nutrient uptake model (BNTM) also appear adequate for accurate predictions of K uptake on these soils of low K-supplying potential, thereby making computations both easier and faster.

Sensitivity analysis indicated that root growth rates and soil solution concentrations of K were the two most important parameters affecting K uptake. The supply of nutrients in these soils, however, was the rate-limiting step to K acquisition by slash pine.

Although this study investigated K uptake by young slash pine seedlings, the potential also exists for simulating

uptake by rotation-aged trees. Before application to mature trees can be accomplished, however, reliable estimates of rooting (including hyphae) densities must be included, together with information on the effect of multiple soil horizons and forest floor on uptake processes.

Application of this mechanistic approach to older trees could be useful for delineating site response to cultural treatments such as fertilization, thereby reducing the need for extensive field trials. Nutrient uptake simulations could also improve our understanding of the long-term effects of intensive harvesting on nutrient pools: a real problem for infertile soils such as are found on the southeastern coastal plain.

## CHAPTER 6 OVERALL CONCLUSIONS

### Major Conclusions

The following is a list of the major conclusions from this research, by chapter:

#### Chapter 2

1. Slash pine genotypes, as classified by seed sources, affected  $I_{\max}$  values for K and Rb uptake as well as the selectivity of the root for K and Rb.
2. The use of Rb as a tracer for K should be done with caution in nutrient uptake studies, not only for slash pine but for other plant species as well, in order to avoid misleading results.
3. The absorption of K plus Rb by slash pine roots was affected by the internal K plus Rb concentrations in root tissues, suggesting some feedback mechanisms for uptake.
4. Variability in Michaelis-Menten parameters for roots in solution cultures may not be important for K modeling in field situations, if diffusion/mass-flow processes are implicated as the rate-limiting step for nutrient uptake.

#### Chapter 3

1. Woody roots are an effective absorbing surface for water and K, especially for seedlings with new shoot growth.

Water, K and Rb absorption expressed per unit root length by woody roots were comparable to or better than that by entire root systems.

2. Potassium uptake predictions, via the Barber-Cushman model, using parameters for both woody and white roots, resulted in K predictions which were similar to those for entire root systems. Potassium uptake was underpredicted for white roots alone, underlying the importance of woody root length.

#### Chapter 4

1. Soil buffer power should be defined as  $+K_d$ , since this definition is conceptually correct under any condition.

2. The use of buffer power defined as  $K_d$  is correct only when the value of  $K_d \gg$  ; otherwise erroneous estimates of solute diffusion and of nutrient replenishment to soil solutions may result.

#### Chapter 5

1. A theoretical approach to nutrient uptake, based on diffusion/mass-flow processes, was adequate for describing K uptake by slash pine seedlings. Predictions were excellent for seedlings at the tree nursery when fertilizer amendments were incorporated. The model was limited in its predictive power at field sites, however, due to the exclusion of uptake by external mycorrhizal hyphae. Pot-binding of seedlings under greenhouse conditions resulted in overpredictions of K uptake.

2. Simplification of the nutrient uptake model (BNTM) by assuming steady-state conditions during each time step was appropriate for predicting K uptake on soils of low K-supplying potential of the southeastern coastal plain.
3. Sensitivity analysis indicated that the amount of root surface area available for nutrient uptake is crucial for obtaining accurate predictions of K uptake on these soils.

#### Future Research

The results of this research evaluated a mechanistic approach for predicting K uptake by slash pine seedlings from soils of low K-supplying potential of the southeastern coastal plain. This work, however, encompassed only one soil horizon and trees that were of seedling age. Such conditions do not exist for rotation-aged trees. Therefore, the gap needs to be closed between uptake from one soil horizon and multiple horizons as observed for Spodosols, and between seedlings and mature trees.

Presently, on-going research by the author is investigating the absorption of K from two soil horizons through the use of K/Rb ratios (Kuhlmann et al., 1985). This method will then be used to validate K uptake from the two horizons by the mechanistic model.

Water is an important factor in nutrient uptake but it wasn't actually addressed in this study per se. Water contents were assumed to be constant (i.e., at steady

state); however, for poorly drained Spodosols, water contents can be affected by fluctuating water tables. Changing water contents can in turn influence estimates of diffusion coefficients, buffer powers, water flux and initial solution concentrations; therefore, incorporating a theoretical approach for predicting water contents in soil profiles, such as has been done by Phillips et al. (1989), will be helpful.

Application of nutrient uptake models to trees will also require reliable estimates of mycorrhizal hyphae and tree rooting densities. Currently, there are empirical approaches for estimating root growth rates (Simmons and Pope, 1988; Diggle, 1988); however, a more mechanistically derived approach is desired.

Lastly, K uptake was the emphasis of this study, but tree nutrition encompasses many macro- and micro-elements. Seedling tissues from this study will also be analyzed for calcium, magnesium, phosphorus and iron and compared with model predictions.

In conclusion, it is hoped that the nutrient-supplying potential of soil horizons, including subsoils, with respect to tree growth and nutrition can be more fully understood through the use of diffusion/mass-flow predictions of nutrient uptake.

APPENDIX A  
SOIL AND PLANT PARAMETERS USED FOR THE SIMULATIONS

The Michaelis-Menten parameters are presented for entire, woody and white root systems for the BCM, and for entire root systems only for the BNTM, in Table A-1.

Tables A-2, A-3, A-4, A-5, and A-6 constitute a list of the soil and plant input parameters for simulations of potassium uptake for the Pomona 1, Pomona 2, GNF Time 1, GNF Time 2, and nursery experiments, respectively.

Simulations for the BCM were run at time and space steps of 200 seconds and 200 cm, respectively. The time step for the BNTM was 0.01 seconds.

Table A-1. Michaelis-Menten parameters for the simulations.

Model	Root Type	$I_{\max}$	$K_m$	$C_{\min}$
		$(\mu\text{mol cm}^{-2}\text{s}^{-1})$ $*10^6$	$\mu\text{mol cm}^{-3}$	$\mu\text{mol cm}^{-3}$
BCM	Entire	3.61	0.0287	0.001
	Woody	2.33	0.0042	0.001
	White	2.96	0.0096	0.001
BNTM	Entire	1.26 <sup>a</sup>		

a  $I_{\max}/K_m$  with units of  $(\text{cm s}^{-1}) * 10^{-4}$ .

Table A-2. Soil and plant input parameters for the Pomona 1 experiment.

Parameter	Simulation					
	1	2	3	4	5	6
$D_e$ ( $\text{cm}^2\text{s}^{-1}$ )* $10^{-7}$	1.01	0.98	1.09	1.00	1.01	1.00
$b^1$	3.64	3.64	3.64	3.64	3.64	3.64
$C_{ii}$ ( $\mu\text{mol cm}^{-3}$ )	0.136	0.136	0.136	0.136	0.136	0.136
$V_o$ ( $\text{cm s}^{-1}$ )* $10^{-6}$	3.18	4.07	2.39	2.55	3.25	2.51
$r_1$ (cm)	1.54	1.56	1.47	1.38	0.97	0.95
$r_o$ (cm)	0.039	0.039	0.04	0.04	0.039	0.039
$L_o$ (cm)	11.85	11.85	11.85	11.85	11.85	11.85
$k$ ( $\text{cm s}^{-1}$ )* $10^{-4}$	1.18	1.15	1.16	1.34	1.83	1.92
$L_v^a$ ( $\text{cm cm}^{-3}$ )	5.9	5.9	5.9	5.9	5.9	5.9
$k^{1a}$ ( $\text{cm cm}^{-3}\text{s}^{-1}$ )* $10^{-8}$	5.89	5.74	5.79	6.66	9.12	9.54
$L_w^b$ (cm)	5.0	5.0	5.0	5.0	5.0	5.0
$k_w^b$ ( $\text{cm s}^{-1}$ )* $10^{-4}$	0.70	0.72	0.78	0.84	1.47	1.67
$L_w^c$ (cm)	6.85	6.85	6.85	6.85	6.85	6.85
$k_w^c$ ( $\text{cm s}^{-1}$ )* $10^{-4}$	0.48	0.43	0.39	0.49	0.36	0.24
Time (days)	25.13	25.23	28.21	28.19	42.06	42.17

Table A-2. Continued

Parameter	Simulation					
	7	8	9	10	11	12
$D_o$ ( $\text{cm}^2\text{s}^{-1}$ )* $10^{-7}$	1.02	1.03	0.98	1.04	1.01	1.01
$b^1$	3.64	3.64	3.64	3.64	3.64	3.64
$C_{11}$ ( $\mu\text{mol cm}^{-3}$ )	0.136	0.136	0.136	0.136	0.136	0.136
$V_o$ ( $\text{cm s}^{-1}$ )* $10^{-6}$	2.83	2.49	2.66	1.04	2.53	2.23
$r_1$ (cm)	1.03	0.95	0.84	0.83	0.97	0.84
$r_o$ (cm)	0.397	0.038	0.038	0.038	0.042	0.039
$L_o$ (cm)	11.85	11.85	11.85	11.85	11.85	11.85
$k$ ( $\text{cm s}^{-1}$ )* $10^{-4}$	1.61	1.93	1.51	1.55	1.12	1.49
$L_v^a$ ( $\text{cm cm}^{-3}$ )	5.9	5.9	5.9	5.9	5.9	5.9
$k^1a$ ( $\text{cm cm}^{-3}\text{s}^{-1}$ )* $10^{-8}$	8.02	9.59	7.50	7.72	5.57	7.44
$L_w^b$ (cm)	5.0	5.0	5.0	5.0	5.0	5.0
$k_w^b$ ( $\text{cm s}^{-1}$ )* $10^{-4}$	1.37	1.74	1.38	1.39	1.06	1.39
$L_w^c$ (cm)	6.85	6.85	6.85	6.85	6.85	6.85
$k_w^c$ ( $\text{cm s}^{-1}$ )* $10^{-4}$	0.24	0.18	0.12	0.16	0.06	0.10
Time (days)	42.21	42.25	68.58	68.54	68.60	68.63

a For the BNTM.

b Woody roots.

c White roots.

Table A-3. Soil and plant input parameters for the Pomona 2 experiment.

Parameter	Simulation					
	1	2	3	4	5	6
$D_e$ ( $\text{cm}^2 \text{s}^{-1}$ ) $\times 10^{-7}$	0.21	0.21	0.21	0.21	0.21	0.21
$b'$	6.11	6.11	6.11	6.11	6.11	6.11
$C_{11}$ ( $\mu\text{mol cm}^{-3}$ )	0.93	0.93	0.93	0.93	0.93	0.93
$V_o$ ( $\text{cm s}^{-1}$ ) $\times 10^{-6}$	10.34	8.51	6.05	5.13	4.37	3.98
$r_1$ (cm)	2.02	1.96	1.75	1.72	0.98	0.96
$r_o$ (cm)	0.043	0.040	0.044	0.041	0.040	0.043
$L_o$ (cm)	11.85	11.85	11.85	11.85	11.85	11.85
$k$ ( $\text{cm s}^{-1}$ ) $\times 10^{-4}$	0.64	0.67	0.78	0.80	1.71	1.79
$L_v^a$ ( $\text{cm cm}^{-3}$ ) $\times 10^{-3}$	5.9	5.9	5.9	5.9	5.9	5.9
$k^a$ ( $\text{cm cm}^{-3} \text{s}^{-1}$ ) $\times 10^{-8}$	3.29	3.49	4.03	4.15	8.81	9.22
$L_w^b$ (cm)	5.0	5.0	5.0	5.0	5.0	5.0
$k_w^b$ ( $\text{cm s}^{-1}$ ) $\times 10^{-4}$	0.49	0.45	0.54	0.61	1.39	1.41
$L_w^c$ (cm)	6.85	6.85	6.85	6.85	6.85	6.85
$k_w^c$ ( $\text{cm s}^{-1}$ ) $\times 10^{-4}$	0.14	0.22	0.24	0.19	0.31	0.38
Time (days)	25.31	25.51	28.17	28.15	42.56	42.59

Table A-3. Continued

Parameter	Simulation					
	7	8	9	10	11	12
$D_e$ ( $\text{cm}^2\text{s}^{-1}$ )* $10^{-7}$	0.20	0.22	0.26	0.22	0.20	0.22
$b^1$	6.11	6.11	6.11	6.11	6.11	6.11
$C_{ii}$ ( $\mu\text{mol cm}^{-3}$ )	0.93	0.93	0.93	0.93	0.93	0.93
$V_o$ ( $\text{cm s}^{-1}$ )* $10^{-6}$	5.01	3.21	3.47	2.93	3.85	2.26
$r_1$ (cm)	0.96	1.05	0.62	0.77	0.62	0.66
$r_o$ (cm)	0.041	0.039	0.036	0.042	0.035	0.042
$L_o$ (cm)	11.85	11.85	11.85	11.85	11.85	11.85
$k$ ( $\text{cm s}^{-1}$ )* $10^{-4}$	1.78	1.49	2.65	1.71	2.64	2.33
$L_v^a$ ( $\text{cm cm}^{-3}$ )* $10^{-3}$	5.9	5.9	5.9	5.9	5.9	5.9
$k^1{}^a$ ( $\text{cm cm}^{-3}\text{s}^{-1}$ )* $10^{-8}$	9.22	7.70	13.71	8.85	13.62	12.03
$L_w^b$ (cm)	5.0	5.0	5.0	5.0	5.0	5.0
$k_w^b$ ( $\text{cm s}^{-1}$ )* $10^{-4}$	1.41	1.16	2.34	1.44	2.37	2.11
$L_w^c$ (cm)	6.85	6.85	6.85	6.85	6.85	6.85
$k_w^c$ ( $\text{cm s}^{-1}$ )* $10^{-4}$	0.37	0.34	0.31	0.27	0.27	0.22
Time (days)	42.63	42.65	69.04	69.04	69.05	69.06

a For the BNTM.

b Woody roots.

c White roots.

Table A-4. Soil and plant input parameters for the GNF Time 1 experiment.

Parameter	Simulation					
	1	2	3	4	5	6
$D_e \text{ (cm}^2\text{s}^{-1}) * 10^{-7}$	2.91	4.35	3.59	6.28	3.33	3.93
$b'$	3.41	3.45	3.43	3.06	3.42	3.44
$C_{li} \text{ (}\mu\text{mol cm}^{-3}\text{)}$	0.048	0.035	0.047	0.060	0.048	0.035
$V_o \text{ (cm s}^{-1}) * 10^{-6}$	3.79	3.79	3.79	3.79	3.79	3.79
$r_1 \text{ (cm)}$	1.74	1.98	1.81	2.09	1.78	1.70
$r_o \text{ (cm)}$	0.049	0.041	0.046	0.044	0.054	0.038
$L_o \text{ (cm)}$	19.40	16.60	20.30	28.90	19.40	16.60
$k \text{ (cm s}^{-1}) * 10^{-5}$	2.42	1.18	5.13	7.37	2.14	2.93
$L_v^a \text{ (cm cm}^{-3}) * 10^{-2}$	6.06	5.72	3.96	2.92	3.36	2.64
$k'^a \text{ (cm cm}^{-3}\text{s}^{-1}) * 10^{-8}$	7.63	4.08	1.00	7.44	3.72	4.64
Time (days)	6.74	6.74	6.73	6.74	20.97	20.97

Table A-4. Continued

Parameter	Simulation					
	7	8	9	10	11	12
$D_e \text{ (cm}^2\text{s}^{-1}) * 10^{-7}$	3.70	4.95	3.45	4.03	3.39	4.02
$b'$	3.43	3.03	3.43	3.44	3.42	3.01
$C_{li} \text{ (}\mu\text{mol cm}^{-3}\text{)}$	0.047	0.060	0.048	0.035	0.047	0.060
$V_o \text{ (cm s}^{-1}\text{)} * 10^{-6}$	3.79	3.79	3.79	3.79	3.79	3.79
$r_1 \text{ (cm)}$	1.76	2.03	2.00	3.14	2.33	2.34
$r_o \text{ (cm)}$	0.042	0.043	0.045	0.060	0.052	0.049
$L_o \text{ (cm)}$	20.30	28.90	19.40	16.60	20.30	28.90
$k \text{ (cm s}^{-1}\text{)} * 10^{-5}$	3.87	9.29	5.17	4.65	5.61	6.78
$L_v^a \text{ (cm cm}^{-3}\text{)} * 10^{-2}$	2.31	1.13	0.74	0.29	0.53	0.61
$k'^a \text{ (cm cm}^{-3}\text{s}^{-1}\text{)} * 10^{-8}$	4.39	3.64	1.98	0.81	1.47	1.44
Time (days)	20.97	20.98	42.00	42.00	42.02	42.02

Table A-4. Continued

Parameter	Simulation		
	13	14	15
$D_e \text{ (cm}^2\text{s}^{-1}) * 10^{-7}$	3.73	3.64	4.03
$b'$	3.43	3.43	3.01
$C_{li} \text{ (}\mu\text{mol cm}^{-3}\text{)}$	0.048	0.047	0.060
$V_o \text{ (cm s}^{-1}\text{)} * 10^{-6}$	3.79	3.79	3.79
$r_1 \text{ (cm)}$	2.33	3.15	2.28
$r_o \text{ (cm)}$	0.044	0.059	0.046
$L_o \text{ (cm)}$	19.40	20.30	28.90
$k \text{ (cm s}^{-1}\text{)} * 10^{-5}$	6.27	4.44	15.14
$L_v^a \text{ (cm cm}^{-3}\text{)} * 10^{-2}$	0.29	0.23	0.19
$k'^a$ $\text{(cm cm}^{-3}\text{s}^{-1}\text{)} * 10^{-8}$	0.92	0.49	0.98
Time (days)	70.02	69.97	70.00

a For the BNTM.

Table A-5. Soil and plant input parameters for the GNF Time 2 experiment.

Parameter	Simulation			
	1	2	3	4
$D_e \text{ (cm}^2\text{s}^{-1}) * 10^{-7}$	3.81	4.33	3.43	3.70
$b'$	3.44	3.45	3.43	3.00
$C_{11} \text{ (}\mu\text{mol cm}^{-3}\text{)}$	0.048	0.035	0.047	0.060
$V_o \text{ (cm s}^{-1}\text{)} * 10^{-6}$	3.79	3.79	3.79	3.79
$r_1 \text{ (cm)}$	1.48	2.16	1.39	2.87
$r_o \text{ (cm)}$	0.040	0.037	0.041	0.044
$L_o \text{ (cm)}$	31.60	30.40	25.10	26.30
$k \text{ (cm s}^{-1}\text{)} * 10^{-4}$	4.57	2.83	5.69	9.42
$L_v^a \text{ (cm cm}^{-3}\text{)} * 10^{-2}$	2.32	1.56	1.78	0.28
$k'^a \text{ (cm cm}^{-3}\text{s}^{-1}\text{)} * 10^{-6}$	3.36	1.23	4.03	0.98
Time (days)	42.08	42.07	42.06	42.03

Table A-5. Continued

Parameter	Simulation			
	5	6	7	8
$D_e \text{ (cm}^2\text{s}^{-1}) * 10^{-7}$	3.83	4.46	3.62	3.67
$b^1$	3.44	3.45	3.43	3.00
$C_{11} \text{ (}\mu\text{mol cm}^{-3}\text{)}$	0.048	0.035	0.047	0.060
$V_o \text{ (cm s}^{-1}) * 10^{-6}$	3.79	3.79	3.79	3.79
$r_1 \text{ (cm)}$	1.71	2.67	2.36	2.25
$r_o \text{ (cm)}$	0.036	0.044	0.036	0.039
$L_o \text{ (cm)}$	31.60	30.40	25.10	26.30
$k \text{ (cm s}^{-1}) * 10^{-4}$	1.02	4.61	1.60	1.84
$L_v^a \text{ (cm cm}^{-3}) * 10^{-2}$	0.53	0.43	0.14	0.14
$k'^a$ $\text{(cm cm}^{-3}\text{s}^{-1}) * 10^{-8}$	1.71	0.66	0.92	1.00
Time (days)	70.31	70.98	70.37	71.00

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a For the BNTM.

Table A-6. Soil and plant input parameters for the nursery experiment.

Parameter	Simulation					
	1	2	3	4	5	6
$D_e$ ( $\text{cm}^2\text{s}^{-1}$ )* $10^{-8}$	5.78	5.78	5.78	5.78	6.81	6.81
$b^i$	6.26	6.26	6.26	6.26	6.27	6.27
$C_{11}$ ( $\mu\text{mol cm}^{-3}$ )	0.203	0.203	0.203	0.203	0.203	0.203
$V_o$ ( $\text{cm s}^{-1}$ )* $10^{-6}$	3.79	3.79	3.79	3.79	3.79	3.79
$r_1$ (cm)	2.59	2.48	2.43	2.46	2.14	1.93
$r_o$ (cm)	0.038	0.042	0.035	0.035	0.026	0.032
$L_o$ (cm)	41.25	41.25	41.25	41.25	41.25	41.25
$k$ ( $\text{cm s}^{-1}$ )* $10^{-4}$	1.40	0.95	0.86	1.19	1.65	2.12
$L_v^a$ ( $\text{cm cm}^{-3}$ )* $10^{-2}$	1.53	2.14	2.35	1.89	1.18	1.18
$k^i{}^a$ ( $\text{cm cm}^{-3}\text{s}^{-1}$ )* $10^{-8}$	5.19	4.87	4.93	5.47	4.72	6.08
$L_w^b$ (cm)	- <sup>c</sup>	20.63	20.63	20.63	-	-
$k_w^b$ ( $\text{cm s}^{-1}$ )* $10^{-4}$	-	0.75	0.72	0.93	-	-
$L_w^d$ (cm)	-	20.63	20.63	20.63	-	-
$k_w^d$ ( $\text{cm s}^{-1}$ )* $10^{-5}$	-	1.70	1.40	2.60	-	-
Time (days)	7.05	7.15	7.15	7.15	14.07	14.08

Table A-6. Continued

Parameter	Simulation					
	7	8	9	10	11	12
$D_e$ ( $\text{cm}^2\text{s}^{-1}$ )* $10^{-8}$	6.81	6.81	6.81	3.32	3.32	3.32
$b'$	6.27	6.27	6.27	6.23	6.23	6.23
$C_{11}$ ( $\mu\text{mol cm}^{-3}$ )	0.203	0.203	0.203	0.203	0.203	0.203
$V_o$ ( $\text{cm s}^{-1}$ )* $10^{-6}$	3.79	3.79	3.79	3.79	3.79	3.79
$r_1$ (cm)	1.65	1.80	2.00	1.63	1.79	1.54
$r_o$ (cm)	0.027	0.036	0.032	0.031	0.036	0.032
$L_o$ (cm)	41.25	41.25	41.25	41.25	41.25	41.25
$k$ ( $\text{cm s}^{-1}$ )* $10^{-4}$	2.99	2.29	2.11	2.36	1.84	2.43
$L_v^a$ ( $\text{cm cm}^{-3}$ )* $10^{-2}$	1.18	1.26	1.09	1.05	1.09	1.14
$k'^a$ ( $\text{cm cm}^{-3}\text{s}^{-1}$ )* $10^{-8}$	8.59	7.04	5.59	6.04	4.86	6.69
$L_w^b$ (cm)	-	-	20.63	20.63	20.63	20.63
$k_w^b$ ( $\text{cm s}^{-1}$ )* $10^{-4}$	-	-	1.50	1.70	1.23	1.62
$L_w^d$ (cm)	-	-	20.63	20.63	20.63	20.63
$k_w^d$ ( $\text{cm s}^{-1}$ )* $10^{-5}$	-	-	6.10	6.62	6.03	8.14
Time (days)	14.09	14.10	14.12	21.08	21.08	21.09

Table A-6. Continued

Parameter	Simulation					
	13	14	15	16	17	18
$D_e$ ( $\text{cm}^2\text{s}^{-1}$ )* $10^{-8}$	3.32	3.32	4.77	4.77	4.77	4.77
$b'$	6.23	6.23	6.25	6.25	6.25	6.25
$C_{11}$ ( $\mu\text{mol cm}^{-3}$ )	0.203	0.203	0.203	0.203	0.203	0.203
$V_o$ ( $\text{cm s}^{-1}$ )* $10^{-6}$	3.79	3.79	3.79	3.79	3.79	3.79
$r_1$ (cm)	1.61	1.68	1.50	1.59	1.53	1.31
$r_o$ (cm)	0.037	0.036	0.034	0.037	0.038	0.039
$L_o$ (cm)	41.25	41.25	41.25	41.25	41.25	41.25
$k$ ( $\text{cm s}^{-1}$ )* $10^{-4}$	2.67	2.26	2.27	2.54	2.30	3.03
$L_v^a$ ( $\text{cm cm}^{-3}$ )* $10^{-2}$	0.96	1.03	0.99	0.79	0.94	0.99
$k'^a$ ( $\text{cm cm}^{-3}\text{s}^{-1}$ )* $10^{-8}$	6.19	5.62	5.45	4.87	5.24	7.27
$L_w^b$ (cm)	20.63	20.63	20.63	20.63	20.63	20.63
$k_w^b$ ( $\text{cm s}^{-1}$ )* $10^{-4}$	1.96	1.64	2.22	2.32	1.96	2.56
$L_w^d$ (cm)	20.63	20.63	20.63	20.63	20.63	20.63
$k_w^d$ ( $\text{cm s}^{-1}$ )* $10^{-5}$	7.14	6.21	5.39	2.21	3.44	4.69
Time (days)	21.11	21.07	28.06	28.06	28.08	28.10

Table A-6. Continued

Parameter	Simulation					
	19	20	21	22	23	25
$D_e$ ( $\text{cm}^2\text{s}^{-1}$ ) $\times 10^{-8}$	4.60	4.60	4.60	4.60	3.45	3.45
$b^1$	6.25	6.25	6.25	6.25	6.24	6.24
$C_{li}$ ( $\mu\text{mol cm}^{-3}$ )	0.203	0.203	0.203	0.203	0.203	0.203
$V_o$ ( $\text{cm s}^{-1}$ ) $\times 10^{-6}$	3.79	3.79	3.79	3.79	3.79	3.79
$r_1$ (cm)	1.06	1.36	1.15	1.19	1.19	1.06
$r_o$ (cm)	0.035	0.038	0.034	0.036	0.036	0.036
$L_o$ (cm)	41.25	41.25	41.25	41.25	41.25	41.25
$k$ ( $\text{cm s}^{-1}$ ) $\times 10^{-4}$	4.12	2.74	3.39	3.25	3.04	3.07
$L_v^a$ ( $\text{cm cm}^{-3}$ ) $\times 10^{-2}$	0.99	0.81	0.92	0.91	0.80	1.00
$k'^a$ ( $\text{cm cm}^{-3}\text{s}^{-1}$ ) $\times 10^{-8}$	9.09	5.39	7.57	7.17	5.92	7.48
$L_w^b$ (cm)	20.63	20.63	20.63	20.63	20.63	20.63
$k_w^b$ ( $\text{cm s}^{-1}$ ) $\times 10^{-4}$	3.25	2.17	2.34	2.53	-	-
$L_w^d$ (cm)	20.63	20.63	20.63	20.63	20.63	20.63
$k_w^d$ ( $\text{cm s}^{-1}$ ) $\times 10^{-5}$	8.69	5.67	10.52	7.25	-	-
Time (days)	35.05	35.07	35.07	35.09	42.05	42.06

Table A-6. Continued

Parameter	Simulation			
	26	27	28	29
$D_o$ ( $\text{cm}^2\text{s}^{-1}$ )* $10^{-8}$	3.45	2.40	2.40	2.40
$b'$	6.24	6.22	6.22	6.22
$C_{11}$ ( $\mu\text{mol cm}^{-3}$ )	0.203	0.203	0.203	0.203
$V_o$ ( $\text{cm s}^{-1}$ )* $10^{-6}$	3.79	3.79	3.79	3.79
$r_1$ (cm)	1.14	1.06	1.06	0.98
$r_o$ (cm)	0.034	0.042	0.040	0.037
$L_o$ (cm)	41.25	41.25	41.25	41.25
$k$ ( $\text{cm s}^{-1}$ )* $10^{-4}$	3.48	3.31	3.93	3.33
$L_v^a$ ( $\text{cm cm}^{-3}$ )* $10^{-2}$	0.78	0.71	0.60	0.83
$k'^a$ ( $\text{cm cm}^{-3}\text{s}^{-1}$ )* $10^{-8}$	6.56	5.70	5.68	6.68
$L_w^b$ (cm)	20.63	20.63	20.63	20.63
$k_w^b$ ( $\text{cm s}^{-1}$ )* $10^{-4}$	-	2.52	3.09	2.53
$L_w^d$ (cm)	20.63	20.63	20.63	20.63
$k_w^d$ ( $\text{cm s}^{-1}$ )* $10^{-5}$	-	7.94	8.37	8.03
Time (days)	42.07	56.07	56.09	56.12

a For the BNTM.

b Woody roots.

c Not measured.

d White roots.

APPENDIX B  
WATER UPTAKE BY WOODY AND ENTIRE ROOT SYSTEMS  
DURING DAY AND NIGHT PERIODS

Table B-1. Average water uptake per pot, per unit root length and per unit root surface area for entire root systems and for woody roots of slash pine during two consecutive days of the Feb. 1987 experiment.

Root Type	Day 1 (0800-1800)	Night (1800-0730)	Day 2 (0730-1700)
	----- cm <sup>3</sup> -----		
All roots	70.5±2.2 <sup>a</sup>	24.8±1.1	60.6±2.3
Woody roots	22.9±2.9 *	24.5±1.8	14.1±2.9 *
	----- cm <sup>3</sup> cm <sup>-1</sup> -----		
All roots	.031±.003	.011±.001	.026±.003
Woody roots	.056±.010	.059±.008 *	.033±.006
	----- cm <sup>3</sup> cm <sup>-2</sup> -----		
All roots	.158±.032	.055±.011	.135±.026
Woody roots	.123±.020	.132±.014 *	.076±.016

a Mean and SE

\* Root treatments significantly different at P=0.05

APPENDIX C  
POTASSIUM DIFFUSION COEFFICIENTS FOR SOILS OF LOW  
POTASSIUM-SUPPLYING POTENTIAL: EVALUATION OF TWO METHODS  
AND IMPLICATIONS FOR NUTRIENT UPTAKE MODELS

Introduction

Mechanistic models have frequently been used to predict nutrient uptake by plants growing under a variety of conditions (Brewster et al., 1976; Silberbush and Barber, 1983, 1984; Mullins et al., 1986; Rengel, 1988). One requirement for accurately predicting nutrient uptake involves an understanding of how ions are transported through the soil to the root surface. Nutrient transport to the root is governed by diffusion and mass flow (Barber, 1962); however, diffusion has been implicated as being the dominant process for potassium transport in most soils (Barber, 1962; Baligar, 1985).

The application of ion diffusion theory to soils was introduced in the early 1960's (Schofield and Graham-Bryce, 1960; Olsen et al., 1962). During this period, diffusion of ions in soils was calculated by measuring the quantity of radioactive ions diffusing across the interface from an initially radioactive diffusion cylinder into an adjacent, unlabeled cylinder during time  $t$  (Porter et al., 1960; Olsen

et al., 1962; Graham-Bryce, 1963; Phillips and Brown, 1964; Rowell et al., 1967).

Since then, two techniques have frequently been used to measure diffusion coefficients ( $D_e$ ) in soil: a direct measurement using an ion-exchange resin paper technique (Vaidyanathan and Nye, 1966; Tinker, 1969), and a theoretical calculation using ion-exchange isotherms (Nye, 1968; Warncke and Barber, 1972b; Mullins and Summers, 1986b). The resin paper technique has been shown to be ineffective for accurate measurements of phosphorus  $D_e$  values (Vaidyanathan and Nye, 1970); however, results were quite reproducible for K (CV=2.4%) (Vaidyanathan and Nye, 1966). Diffusion coefficients for nutrient uptake modeling have been almost exclusively calculated by using buffer powers, from exchange isotherms.

The purpose, therefore, of this study was to (i) contrast potassium (K) diffusion coefficients measured by the ion-exchange resin paper technique to those calculated from ion exchange isotherms, and (ii) discuss the implications for nutrient uptake modeling.

#### Materials and Methods

Soils in this study were obtained from three sites:

- 1) the surface soil of a Millhopper sand (loamy, siliceous, hyperthermic Grossarenic Paleudults) at the tree nursery near Archer, FL,

- 2) the A horizon of a Pomona fine sand (sandy, siliceous, hyperthermic Ultic Haplaquods) from a 4-year old (Pomona 1) and a 25-year old (Pomona 2) slash pine plantation located near the "Gator National Forest" (GNF), 10 km NE of Gainesville, FL, and
- 3) from two locations (Rep 1 and Rep 2) on a cleared bed within the GNF.

The soils in this study correspond to those used in the modeling of potassium uptake as described in Chapter 5. All soils were air-dried and passed through a 2 mm sieve.

The soils were analyzed for pH, CEC, OM, exchangeable K and extractable K (Table C-1). Bulk densities were determined from intact cores taken in the field. The pH was determined in double-distilled water using a 1:2 soil to solution ratio. Organic matter was determined by the Walkey-Black procedure (Nelson and Sommers, 1982). Exchangeable K was determined by extracting the soil with  $\text{NH}_4\text{OAc}$  (Knudsen et al., 1982), while extractable K was measured using the Mehlich-I solution ( $0.025 \text{ N H}_2\text{SO}_4 + 0.05 \text{ N HCl}$ ) with a 1:10 soil-extractant ratio. CEC was measured by the barium chloride method described by Hendershot and Duquette (1986).

#### D. Measurements by the Exchange Resin Paper Technique

Diffusion coefficients were determined by measuring the rate of ion diffusion to  $\text{H}^+$ -saturated cation-exchange resin paper as described by Vaidyanathan and Nye (1966). Soil was packed into glass rings (2 by 4.4 cm) according to their field

Table C-1. Soil characterization data.

Soil	Bulk Density g cm <sup>-3</sup>	pH	OM %	CEC cmol kg <sup>-1</sup>	Exchangeable K			Extractable K	
					NH <sub>4</sub> OAc	Buffer curve	μg g <sup>-1</sup>	Buffer curve	Mehlich I
Pomona 1	1.42	4.02	4.62	2.57±0.28	16.93±0.31	14.55±0.47	12.8±0.5		
Pomona 2	1.47	4.03	1.94	1.43±0.03	8.68±0.43	11.69±1.21	6.7±0.1		
GNF REP1	1.45		3.63	2.00±0.05	5.71±0.08	5.01±0.08	5.2±1.8		
REP2	1.45		3.63	2.05±0.07	6.88±0.12	4.69±0.04	5.2±1.8		
Nursery	1.58	5.63	1.65	1.24±0.05	23.30±0.39	19.67±0.82	19.4±4.0		

bulk densities, saturated with distilled water and then placed on porous tension plates. This process was replicated 3 times for each soil at each of five water tensions - 25, 35, 50, 75 and 100 cm of water. Once the soils had attained the appropriate water tension (usually within 3 days), the cores were allowed to equilibrate in a desiccator containing a dish of water for an additional 24 hours.

The  $H^+$ -saturated cation-exchange resin paper was moistened with distilled water and placed on a piece of plexiglass in the desiccator. The cores were then placed on top of the exchange paper and the soil was lightly pressed down with a rubber stopper to ensure good contact between the paper and soil. A diffusion period of 4 hours was used for all soils. The paper was then removed, rinsed 3 times with 5 ml of 0.1 N HCl, and the solution analyzed for K by atomic absorption spectroscopy.

Diffusion coefficients were then calculated by:

$$D_e = M^2\pi/4C^2t \quad [1]$$

where  $D_e$  is the effective diffusion coefficient ( $cm^2s^{-1}$ ),  $M$  ( $\mu mol\ cm^{-2}$ ) is the total amount of ions that have diffused to the paper in time  $t$ , and  $C$  ( $\mu mol\ cm^{-3}$ ) is the total exchangeable K content of the soil. Diffusion coefficients were determined with  $C$  taken as the exchangeable K measured by  $NH_4OAc$  or as the exchangeable K estimated from the desorption isotherms. Eq. [2] assumes that  $D_e$  is constant with time. Preliminary measurements (not shown) showed that

K diffusion was relatively constant for a diffusion period of 4 hours.

Diffusion coefficients were also measured in the field at the GNF using the exchange paper technique. After the soil surface was cleared of any debris, moistened exchange paper was placed on the soil surface and covered with a plexiglass lid. Experiments were done early in the morning. After 4 hours, the papers were removed and soil samples were taken to measure volumetric water contents. Potassium concentrations and  $D_e$  values were calculated as described above.

#### $D_e$ Calculations From Ion-Exchange Isotherms

Calculated  $D_e$  values based on the theoretical expression of Nye (1966b) were calculated by:

$$D_e = D_L \theta f / b' \quad [2]$$

where  $D_L$  is K diffusion coefficient in water ( $1.58 \times 10^{-5} \text{ cm}^2/\text{s}$ ),  $\theta$  is the volumetric water content ( $\text{cm}^3/\text{cm}^3$ ),  $f$  is the impedance factor which accounts for the tortuous pathway of ions in soil pore sequences, and  $b'$  is the buffer power (see Chapter 4). Diffusion through the adsorbed phase was assumed to be negligible.

Potassium desorption isotherms were developed by a dilution method. Varying amounts of soil were combined with 40 ml of a 0.16mM solution (electrical conductivity (EC) at  $22^\circ\text{C} = 46 \text{ } \mu\text{mhos}$ ) of  $\text{CaCl}_2$ , adjusted to a pH of 4.5, to yield soil-solution ratios of 1:5, 1:10, 1:20, and 1:40. Each soil was replicated at each dilution. Solutions were placed on a

rotary shaker for 24 hours and then filtered through Whatman #1 filter paper. The filtrate was then analyzed for EC and K concentration by atomic absorption spectroscopy with 2% Cs to suppress ionization. Electrical conductivities were used to estimate activity coefficients (Lindsay, 1979), in order to calculate K activities. Differences between K activities and K concentrations were less than 3%, making them essentially the same. The K released into solution ( $\mu\text{mol g}^{-1}$ ) and the K activities ( $\mu\text{M}$ ) were used to plot desorption isotherms. Buffer powers ( $b'$ ) were calculated as:

$$b' = \theta + \theta K_d \quad [3]$$

where  $\rho$  is the bulk density ( $\text{g cm}^{-3}$ ) and  $K_d$  is the slope of the isotherm ( $\text{cm}^3\text{g}^{-1}$ ). Exchangeable K was also estimated from the y-intercept of the isotherms to be used in Eq. [1].

Impedance values were determined by a non-linear least squares procedure (SAS Institute Inc., 1982a) using impedance factors and  $\theta$  data from the literature (Fig. C-1). The impedance factor is described by:

$$f = 3.1\theta^{1.9}. \quad [4]$$

In addition to Eq. [2],  $D_e$  values were also calculated by:

$$D_e = D_L \theta f / b \quad [5]$$

where  $b = \rho K_d$  as explained in Chapter 4.

### Results

Values of  $D_e$  calculated by Eq. [2], using exchangeable K as measured from buffer curves and with  $\text{NH}_4\text{OAc}$ , exhibited a

Figure C-1. Impedance factor for this study (fitted line) as determined from literature data.



good relationship between the logs of the two measurements (slope NS different than 1,  $P=0.05$ ) (Fig. C-2). Values of  $D_e$  for the Pomona 2 soil, using exchangeable K from buffer curves alone, were below the 1:1 line whereas values for the other soils were above the 1:1 line. The Pomona 2 values were lower due to the higher values of exchangeable K as inferred from the buffer curves compared with extraction by  $\text{NH}_4\text{OAc}$  (Table C-1). The manner in which diffusion coefficients increased with increasing water contents is presented in Fig C-3.

Buffer powers as defined as  $b'$  and  $b$  (Table C-2) were used to calculate  $D_e$  from Eqs. [2] and [5], respectively. Diffusion coefficients from the two methods were highly correlated ( $r^2=.99$ ); however,  $D_e$  values from Eq. [5] were 11% higher (significantly different from 1,  $P=0.05$ ) than those from Eq. [2] (Fig. C-4). Deviations from the 1:1 line were more apparent at the highest water contents.

Diffusion coefficients calculated from Eq. [2] were 5 to 11 times larger at intermediate water contents ( $0.12-0.26 \text{ cm}^3 \text{ cm}^{-3}$ ) and similar ( $< 4$  times) at lower and higher water contents compared to measured  $D_e$  values (Eq. [1]) (Fig. C-5). These results were similar for all soils. Under field conditions, theoretical  $D_e$  values compared favorably with values from the exchange resin paper method (Fig C-6). This result is in opposition to the comparison between theoretical  $D_e$  estimates in the field and  $D_e$  values measured in the

Figure C-2. Comparison of measured  $D_e$  values (Eq. [1]) for sieved soils using exchangeable K values from  $NH_4OAc$  extractions or from exchange isotherms (buffer curves).

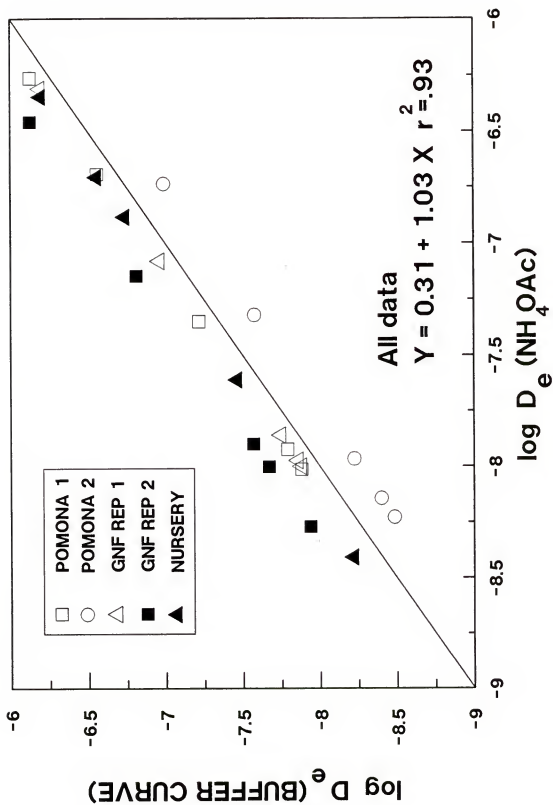


Figure C-3. Measured  $D_e$  values (Eq. [1], exchangeable K from  $\text{NH}_4\text{OAc}$  extractions) for a range of water contents.

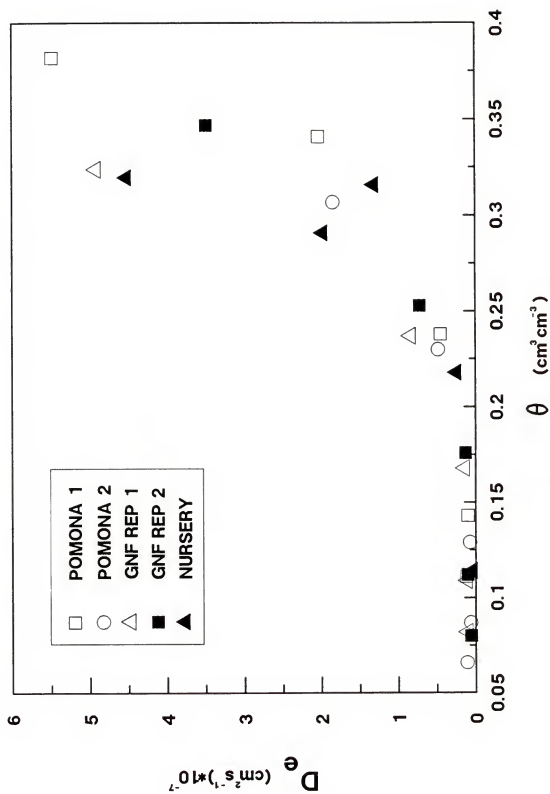


Table C-2. Buffer powers as defined by  $b$  and  $b'$  for a range of soils and water contents.

Soil	$\theta$ $\text{cm}^3 \text{cm}^{-3}$	$b$ $(\rho K_d)$	$b'$ $(\theta + \rho K_d)$
Pomona 1	0.382	$3.47 \pm 0.31$	3.85
	0.341		3.81
	0.238		3.71
	0.143		3.61
	0.111		3.58
Pomona 2	0.307	$5.99 \pm 0.17$	6.30
	0.230		6.22
	0.129		6.12
	0.087		6.08
	0.066		6.06
GNF REP 1	0.324	$3.17 \pm 0.41$	3.49
	0.237		3.41
	0.168		3.34
	0.109		3.28
	0.082		3.25
GNF REP 2	0.347	$2.75 \pm 0.85$	3.10
	0.253		3.00
	0.176		2.93
	0.112		2.86
	0.080		2.83
Nursery	0.320	$6.09 \pm 0.61$	6.41
	0.316		6.41
	0.291		6.38
	0.218		6.31
	0.114		6.21

Figure C-4. Comparison of theoretical  $D_e$  values when the buffer power is defined as  $b'$  (Eq. [2]) and as  $b$  (Eq. [5]). The  $x=y$  line represents a 1:1 relationship.

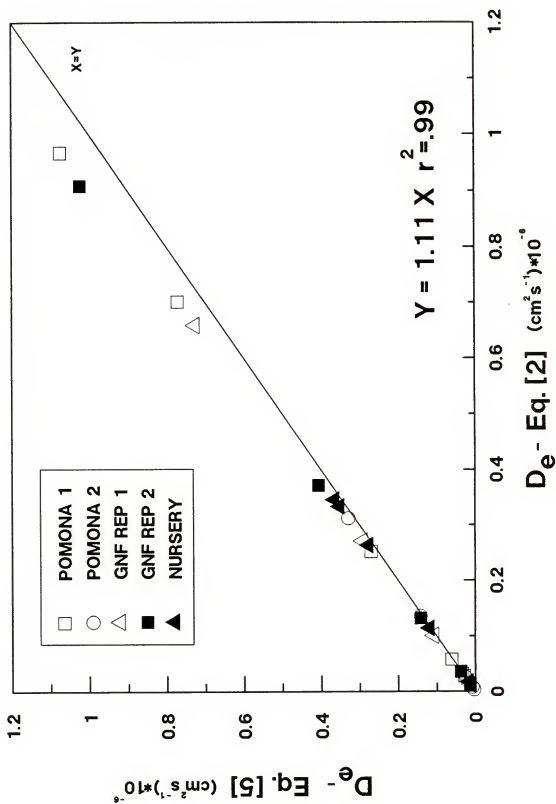


Figure C-5. Ratios of theoretical  $D_e$  values (Eq. [2]) to measured values (Eq. [1], exchangeable K using  $\text{NH}_4\text{OAc}$  extractions) for sieved soil samples over a range of water contents.

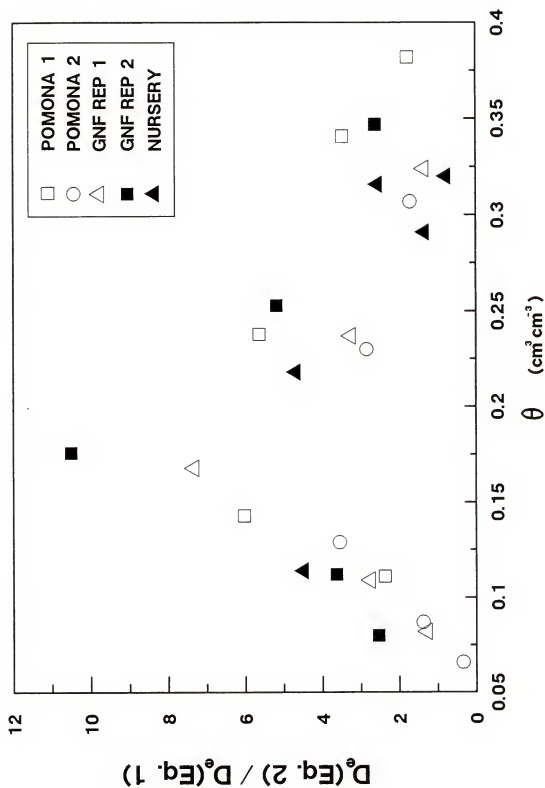
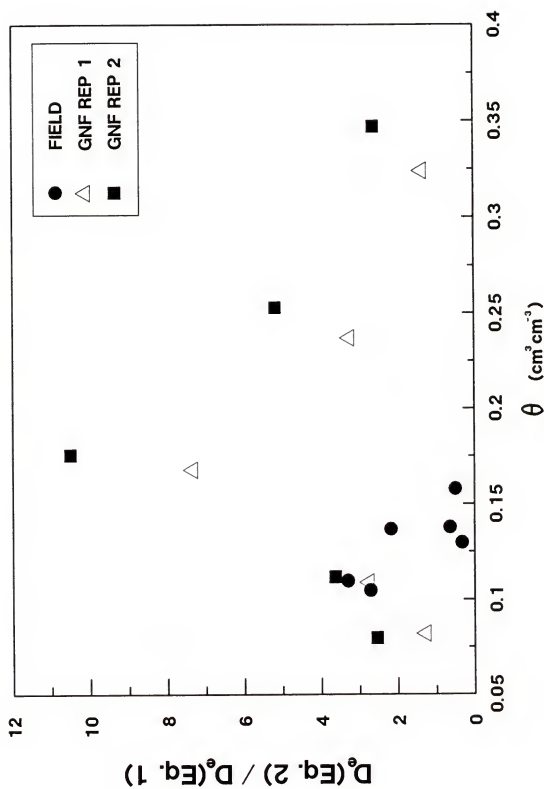


Figure C-6.

Ratio of theoretical  $D_e$  values (Eq. [2]) to measured values (Eq. [1]), exchangeable K using  $\text{NH}_4\text{OAc}$  extractions) over a range of water contents. Diffusion coefficients for Reps 1 and 2 are for sieved soils from the field, whereas  $D_e$  values from the field (\*) represent in-situ field measurements of diffusion.



laboratory on disturbed soil samples from the field (Reps 1 and 2) (Fig. C-6).

### Discussion

Measured diffusion coefficients by the exchange resin paper technique are a simple and efficient means for determining  $K D_e$ , not only in the laboratory but also for direct measurements in the field. Diffusion coefficients by Eq. [2] are also simple to calculate, depending on the availability of ion-exchange isotherms and appropriate estimates of impedance factors.

Although calculated values of  $D_e$  were somewhat higher than measured  $D_e$  values, the agreement between the two methods is rather good despite the fact that impedance factors taken from the literature were from heavier-textured soils than used in this study. Calculated values of  $D_e$  have been reported to be larger (2 to 2500 times) than those measured by the exchange resin paper method for zinc and cadmium (Mullins and Sommers, 1986b) and 5.5 to 18.2 times larger for zinc (Warncke and Barber, 1972b). For potassium, estimates of  $D_e$  by the two methods varied by only 0.76-4.46 times; however, measured values were larger than calculated values of  $D_e$  (Baligar and Barber, 1978c). Therefore, either method would be satisfactory for calculating  $K$  diffusion coefficients.

The better agreement between the two methods for the field data (Fig C-6) suggests that the pore sequences

described by the impedance factors in the field may be more similar to those from the literature than impedance factors for samples in the laboratory. Barraclough and Tinker (1982) have shown that impedance factors were different for sieved and undisturbed samples when studying bromide diffusion. However, absolute measurements of ion impedance for these sandy soils is needed to further understand the effect of impedance factors on ion diffusion.

Buffer powers, when defined as  $b$ , have been shown to be valid for calculating diffusion coefficients using Eq. [5] only when  $\rho K_d > 30$  (see Chapter 4). Otherwise, at values of  $\rho K_d < 30$ ,  $D_e$  values could be overestimated compared to correct estimates by Eq. [2], using  $b'$ . Values of  $\rho K_d$  for K in this study were  $< 6$  and, over a range of water contents,  $D_e$  by Eq. [5] was 11% higher than values from Eq. [2].

Although the differences between measured and calculated  $D_e$  values or between calculated  $D_e$  values using  $b$  and  $b'$  appear small, accurate estimates of  $D_e$  are important for modeling K uptake. Diffusion is a rate-limiting factor for K uptake on these soils of low K-supplying potential (Chapter 5). Sensitivity analysis from Chapter 5 showed that K uptake can be increased by 47% or decreased by as much as 26% when  $D_e$  is changed by a factor of 2 and 0.5, respectively.

These data are as yet inconclusive, since field measurements of  $D_e$  do not cover a wide range of water

contents. Further field measurements are planned to augment this evaluation.

### Conclusions

Measured  $D_e$  values by the exchange resin paper method were similar when exchangeable K was determined either by  $\text{NH}_4\text{OAc}$  extractions or extrapolated from ion exchange isotherms. Diffusion coefficients calculated from the theoretical expression, however, were higher than values measured on disturbed laboratory cores, which may result in higher predicted K uptake when using nutrient uptake models.

Since the theoretical expression for  $D_e$  is frequently used in nutrient uptake models, accurate measurements of impedance factors would improve estimates of  $D_e$  for these sandy soils.

# APPENDIX D CALCULATING SOIL WATER CONTENTS FROM WATER POTENTIALS

Soil moisture release curves were determined by using Tempe cells similar to those described by Klute (1986). Undisturbed samples were taken from the surface horizons in the GNF and the tree nursery. Samples were slowly saturated from the bottom and then installed in Soil Moisture model #1400 pressure Tempe cells with 49.0 kPa (1/2 bar) ceramic plates. Pressure was applied with compressed air. Tempe cells were weighed 3 days after each pressure increase.

Soil moisture-release curves relating water content and water potential were described by the following equation (van Genuchten, 1978):

$$\theta = \theta_r + [(\theta_s - \theta_r) / (1 + (ah)^n)^{(1 - 1/n)}] \quad [1]$$

where  $\theta$  is the volumetric water content ( $\text{cm}^3\text{cm}^{-3}$ ),  $\theta_r$  is the residual volumetric water content ( $\text{cm}^3\text{cm}^{-3}$ ),  $\theta_s$  is the saturated volumetric water content ( $\text{cm}^3\text{cm}^{-3}$ ),  $a$  is a fitted empirical constant ( $\text{cm}^{-1}$ ),  $n$  is a dimensionless fitted empirical constant, and  $h$  is the soil water potential (cm).

The parameters  $\theta_r$ ,  $a$  and  $n$  were fitted by a least squares procedure to the observed moisture-release curve and are presented in Table D-1.

Table D-1. Fitted parameters to determine water contents from soil water potentials.

Parameter	GNF	Nursery
$\theta_s$	0.352	0.306
$\theta_r$	0.147	0.078
a	0.032	0.016
n	2.648	3.345

APPENDIX E  
MODEL ASSUMPTIONS AND BOUNDARY CONDITIONS

Barber-Cushman Model (BCM)

Assumptions

The Barber-Cushman model was developed based on the following assumptions:

1. The soil medium is homogeneeneous and isotropic.
2. Soil moisture conditions are maintained in a steady state (or averaged to approximate steady state) and any moisture gradients perpendicular to the root are not taken into consideration.
3. Nutrient uptake occurs only from solution at the root surface (i.e., no other sources or sinks exist, either through root exudates or microbial activity).
4. Nutrient transport in the soil is by diffusion and mass flow in the radial direction only. Dispersion is negligible.
5. The roots are smooth cylinders of constant radius, with no root hairs or mycorrhizae.
6. The rate of uptake ( $I_n$ ) can be described by Michaelis-Menten kinetics.
7. Diffusion coefficients ( $D_e$ ) and buffer powers ( $b'$ ) are independent of ion concentration in solution.

8. Desorption isotherms are linear, reversible and instantaneous over the range of  $C_i$  and  $C_s$ .
9. Influx characteristics of the root do not change with root or plant age.
10. Nutrient influx is independent of water influx.

#### Boundary Conditions for the BCM

The initial condition for solving the model is:

$$C_{li} = C_r \text{ at } t=0 \quad [1]$$

where  $C_{li}$  and  $C_r$  are the ion concentration in solution initially and the ion concentration at the root surface, respectively.

The inner boundary condition at the root surface, using the Michaelis-Menten equation is:

$$(D_e b') \partial C_l / \partial r + V_o C_l = I_{\max} (C_l - C_{\min}) / [K_m + (C_l - C_{\min})] \quad [2]$$

$$\text{at } r=r_r, \quad t>0$$

where  $r$  is the radial distance from the root axis,  $V_o$  is the water flux,  $I_{\max}$  is the maximum ion influx rate,  $K_m$  is defined as the ion concentration at  $\frac{1}{2}I_{\max}$ ,  $C_{\min}$  is the ion concentration where net influx is zero, and  $r_r$  implies that the radial distance of concern is at the root surface.

The outer boundary condition, assuming interroot competition, is:

$$(D_e b') \partial C_l / \partial r + V_o C_l = 0 \text{ at } r=r_1, \quad t>0. \quad [3]$$

Water is allowed to pass across the outer boundary.

Baldwin-Nye-Tinker Model (BNTM)Assumptions

All assumptions of the BCM apply to the BNTM, except for the 6th assumption. Other assumptions include:

1. Nutrient influx is described by a constant  $\alpha = I_{\max}/K_m$ , when  $K_m \gg C_1$ . Therefore, at low values of  $C_1$ ,

$$I_n = \alpha C_1. \quad [4]$$

2. The concentration-distance profile during depletion away from the root develops in a stepwise manner with time, with each time step approximating a steady-state profile.
3. The depletion zone moves radially from the root until it coincides with the outer boundary defined by  $r_1$ .

Boundary Conditions for the BNTM

The initial boundary condition is the same as [1] for the BCM.

The inner boundary condition is:

$$(D_e b') \partial C_1 / \partial r + V_o C_1 = \alpha C_1 \text{ at } r=r_r, \quad t>0. \quad [5]$$

The outer boundary condition is defined as:

$$\partial C / \partial r = 0 \text{ at } r=r_1, \quad t>0 \quad [6]$$

where no water or nutrients cross the outer boundary.

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## BIOGRAPHICAL SKETCH

Kenneth Cornelius Jacob Van Rees, son of Dutch parents, ALP and Thea Van Rees, was born on April 5, 1958, in Guelph, Ontario, Canada. Ken developed a keen interest for the outdoors from camping on family vacations to fishing for that elusive trout in nearby streams. One of the most important decisions Ken made as a teenager was to allow Jesus Christ to be his Lord and Saviour. After graduation from Fergus High School in 1977, Ken's continued interest in the outdoors lead him to the "bush" country of Northern Ontario, where he enrolled in the forestry program at Lakehead University, Thunder Bay, Ontario. In April, 1981, he graduated with honours with a Bachelor of Science in Forestry degree.

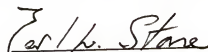
With an interest in forest soils and a change of climate, he moved to "Gator Country" and enrolled at the University of Florida. Ken graduated with a Master of Science degree in December, 1984 and decided to "acquire tenure" by completing his Ph.D in the same field of study.

Kenneth Van Rees met his wife Lois Margaret (Weeks) Van Rees (formerly of Miami, Florida) in the outdoors on a church canoe trip down the Oklawaha River. They have been blessed with one precious girl, Melissa Margaret, and another due in December, 1989.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
Nick B. Comerford, Chair  
Associate Professor of  
Soil Science


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Earl L. Stone  
Professor of Soil Science

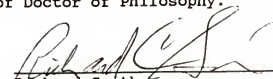
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P. Suresh C. Rao  
Professor of Soil Science

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Brian L. McNeal  
Professor of Soil Science

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Richard Smith  
Professor of Botany

This dissertation was submitted to the Graduate Faculty of the College of Education and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

August 1989

  
Dean, College of Agriculture

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